Hipparion pomeli sp. nov from the late Pliocene of Ahl al Oughlam, Morocco, and a revision of the relationships of Pliocene and Pleistocene African hipparions

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This paper addresses three points: 1) the description of a new species (*H. pomeli* sp. nov.) of Late Pliocene hipparion from Morocco; 2) preliminary notes on hipparion skulls from Langebaanweg E Quarry (*H. hendeyi* sp. nov.) and Chad Kossoum Bougoudi; 3) a new interpretation of African hipparion relationships. The Appendix presents practical techniques allowing the estimation of adult dimensions in juvenile skulls and correlations between two mandibular and skull dimensions. *H. pomeli* was a medium-sized species related to, but smaller than, *H. hasumense* from East Africa. The distance vomer–basion was small and there was no reduction of the third incisors. The lower cheek teeth were caballine, moderately hypsodont, with moderate ectostylids. The limb proportions were cursorial. *H. pomeli* differed from the true *'Eurygnathohippus'* (*H. afarense* and *H. cornelianum*) by the basi-cranial proportions and the lack of reduction of the third incisors. *H. hendeyi* had an extremely short vomer–basion distance, a short distance between the orbit and the POF, primitive teeth, and slender limb bones. It cannot be derived from *H. africanum* or from *H. turkanense.* The greatest resemblances are with (the much smaller) *H. moldavicum* of Taraklia and *H. giganteum* of Grebeniki. The tentative reconstruction of *H. feibeli*'s skull indicates a possible relationship with *H. hendeyi.* The very large skull from Kossoum Bougoudi, Chad, resembles, but is much larger than, the Chinese *H. dermatorhinum*; its dimensions are compatible with the European *H. crassum* and the Mongolian *H. tchicoicum.* It is proposed that more than two migrations gave rise to the various African species of hipparions.

Keywords: Equidae, Mammalia, Hipparion, phylogeny, Africa, Morocco.

INTRODUCTION

Pliocene and Pleistocene hipparions are relatively well documented in East Africa, but till now they were very poorly known in the Maghreb. The late Pliocene hipparion of Ahl al Oughlam is the first represented by skull, teeth and limb bones.

Ahl al Oughlam is a karst and fissure filling near Casablanca that has yielded a very rich fauna of micro- and macromammals (Raynal *et al.* 1990, 2001; Geraads 1993, 1995, 1996, 1997, 2002, 2004a,b, 2006; Alemseged & Geraads 1998; Geraads & Amani 1998; Geraads *et al.* 1998; Geraads & Metz-Muller 1999) together with some fishes, reptiles (Bailon 2000) and many birds (Mourer-Chauviré & Geraads, in press). The sediments are not stratified, and the faunal sample is homogeneous, showing that the filling of the fissures was virtually instantaneous. Biochronological comparisons with East Africa suggest an age of *c.* 2.5 Ma, thus roughly contemporaneous with Omo Shungura Member D, or the gap in the Koobi Fora succession.

SYSTEMATIC PALAEONTOLOGY

Family Equidae Gray, 1821
Genus *Hipparion* De Christol, 1832

***Hipparion pomeli* sp. nov.**, Figs 1, 8, 23

Holotype. AaO-3647, skull, virtually complete but transversely crushed.

Type locality. Ahl al Oughlam, Casablanca, Morocco. About 2.5 Ma.

Diagnosis. A Hipparion of medium size; basion to vomer distance short; muzzle moderately long and wide; faint POF 50 mm in front of the orbit. Incisor arcade rounded. Cheek teeth large, moderately hypsodont; lower cheek teeth caballoid, with moderate ectostylid but sometimes an accessory one.

Etymology. In acknowledgement of Auguste Pomel's prominent contributions to the palaeomammalogy of North Africa.

Description

Skull. AaO-3647 (Fig. 1A) is the skull of an adult male (canines 12 mm long; all teeth erupted but not very worn). It is entire but distorted by lateral crushing. Most of the interesting featured can nevertheless be noted. The size is medium, the basion to vomer distance is short, the muzzle moderately long and wide. There is a faint POF 50 mm in front of the orbit. Comparisons are made with other hipparion skulls by ratio diagrams, taking the average *H. dietrichi* skull from Samos as reference; the corresponding data are given in Table 1. Some of the dimensions used in the ratio diagrams represent the supposed adult state, estimated from juvenile skulls (KNM ER 3539, Olduvai BK II-283). Some muzzle dimensions were also estimated from mandibles (AL 177-21, KNM ER 1626, Omo C, COR 679). Data and explanations are given in the Appendix.

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Figures 2 and 3 are ratio diagrams comparing the Moroccan skull to other hipparions. In Africa, AaO-3647, although smaller, resembles AL-340-8 from the Denen Dora member of the Hadar Formation (Eisenmann 1976, plate 1). Bernor & Armour-Chelu (1997) referred the latter to *H. hasumense* (described on lower cheek teeth from locality 204, Tulu Bor member, East Turkana, Eisenmann 1983) and noted similarities with WW-1528-92 of Wembere Manonga. WW 1528-92, appears to have a longer muzzle but is otherwise quite similar. Other specimens that present some resemblances were found in the Denen Dora and Kada Hadar members of Hadar, and possibly in Member C of Shungura Formation. BKII-2845/6 of Olduvai, unfortunately distorted, seems also rather similar.

The next ratio diagrams (Figs 4 & 5) illustrate the pattern of a second group of late African hipparions. The main difference is in the shape and position of the posterior border of the vomer relatively to the basion and the posterior border of palate (measurements nos. 4 and 3). The vomer–basion distance is much longer. As far as we know, such 'hypercaballine' proportions are unique. Moreover, in the adult type skull (AL 363-18) of *H. afarense* from Hadar KH and in the juvenile skull KNM ER-3539, the vomer has an acute V-shaped posterior border and an acute median ridge (Eisenmann 1976, plates 2 & 3). In probable correlation with the long vomer–basion distance, the Postorbital line (no. 24) looks longer relative to the Anteorbital line (no. 23). In addition, the muzzle width (no. 15) is very large when compared to the cheek teeth and muzzle lengths (nos. 9 & 1), reminding of *H. dietrichi* of Samos.

Scatter diagrams (Figs 6 & 7) illustrate the differences between the two groups. The corresponding data (including those that were not plotted) are given in Table 2.

Thus, in a very schematic way, at least two groups of skulls may be distinguished:

1. *H. hasumense* group: *H. hasumense* (Hadar AL 340-8 and Wembere Manonga WW 1528/92) and *H. pomeli* (AaO-3647 and Olduvai BK II-2845/6). The muzzle is long and narrow; the basion to vomer distance is short; the cheek teeth are relatively large. We refer to *H. hasumense* the Hadar skulls and skull fragments AL 116-115, AL 155-6, AL 164-3, AL 241-18, possibly AL 142-18, and the mandibles AL 177-21 [the latter was first referred to *H. afarense* by Eisenmann, but we presently agree with Bernor & Armour-Chelu (1999a) that it belongs to the *H. hasumense* group]; Omo 18-1968-363 and Omo 18-1969-90. Thus the group is documented, besides Ahl al Oughlam, in the Hadar Formation, SH2, DD, and KH 1–2 members; Wembere-Manonga Valley, Kilolei member; Shungura Formation member C; Olduvai BK II.
2. *H. afarense* group: *H. afarense* (Hadar AL 363-18, and probably AL 164-3) and *H. cornelianum* (East Turkana KNM ER-3539). The vomer has an acute V-shaped posterior border and an acute median ridge; the basion to vomer distance is long; the muzzle is short and wide; the cheek teeth are relatively small. These two species differ mostly by the degree of reduction of the third incisors. We refer to *H. cornelianum* the skull fragments Olduvai BK II-264, BK II-283, BK II-067/5465, and the mandibles or fragments of mandibles Hadar AL 59-9, East Turkana KNM ER-1626; Omo 118-1972-5; Olduvai no no. (Leakey 1965, plate 20), Olduvai 067/5344, Olduvai 1955-293; Cornelia Cor 679. This group is documented in the Hadar Formation, KH 2-3 member; East Turkana Formation, Burgi member; Shungura Formation, member F; Olduvai Bed II; Cornelia.

None of these skulls has a real POF, but some of them exhibit a more or less marked depression a few centimetres in front of the orbit. It may be clearly seen on the Olduvai skull illustrated by Hooijer (1975, plate 7-1) and on AL 241-18 of Hadar. In both groups the lower cheek teeth are caballine and with ectostylids.

Mandible. AaO-197 is a left mandible without the symphyseal part (Fig. 8B2). The cheek tooth series is 159 mm long and the length of the ascending ramus behind the cheek series is 129 mm. The heights are: *c.* 60 mm in front of p2 and 70 mm below p4.

Incisors. The upper, not very worn, incisors of the skull AaO-3647 are large (Fig. 1A2). From I1 to I3 the mesio-distal diameters are *c.* 18, 22 and 19 mm. The incisival arcade is rounded and not very wide, because the I3 are placed behind the I2. Their position does not seem to result from postmortem deformation but from premaxillaries that are too small to accommodate large incisors. The maximal incisor arcade width (across the I2s) is 65 mm. A prominent ridge is visible on the labial surface of the left I3. On the occlusal surface, it comes in contact with the distal border of I2.

Another complete set of not very worn upper incisors is AaO-2104. From I1 to I3 the maximal heights are 68, 64, and *c.* 55 mm; the mesio-distal diameters are 21, 21, and *c.* 22 mm; the labio-lingual diameters are 10, 11, and 9.5 mm. There again, the I3s were placed behind the I2s as shown by a clear indentation along the distal buccal border of the I2s. At mid-crown, the diameters are 15 × 13 on I1, 16.5 × 14 on I2, and 15 × 11 on I3.

Even in *Equus*, the distinction between upper and lower incisors may be difficult, and it is even more so in hipparions. Most of the isolated incisors, often fragmentary, from AaO cannot be sorted with certainty. But it is clear that during their wear they did not remain wide (mesio-distally) and shallow (labio-lingually) for as long a time as those of *H. afarense s.l* and *H. cornelianum.* On the other hand, when they are only slightly worn, their width is much larger than in AL 155-6 (also slightly worn) from the Denen Dora member, and more like AL 177-21 (even less worn and also from Denen Dora). In the Shungura Formation, the more similar incisors are from unit C8 (Eisenmann 1985, plate 1-1).

Permanent upper cheek teeth. Eight individuals are represented by complete series or associated teeth (Fig. 1A3,B, C; Table 3). There are moreover 20 isolated cheek teeth (Table 4). The sample looks homogeneous. The teeth are moderately or very plicated, with plis caballins ranging in number from one to four. Protocones are lenticular or lingually concave (Eisenmann *et al.* 1988, fig. 5C4,C6). In

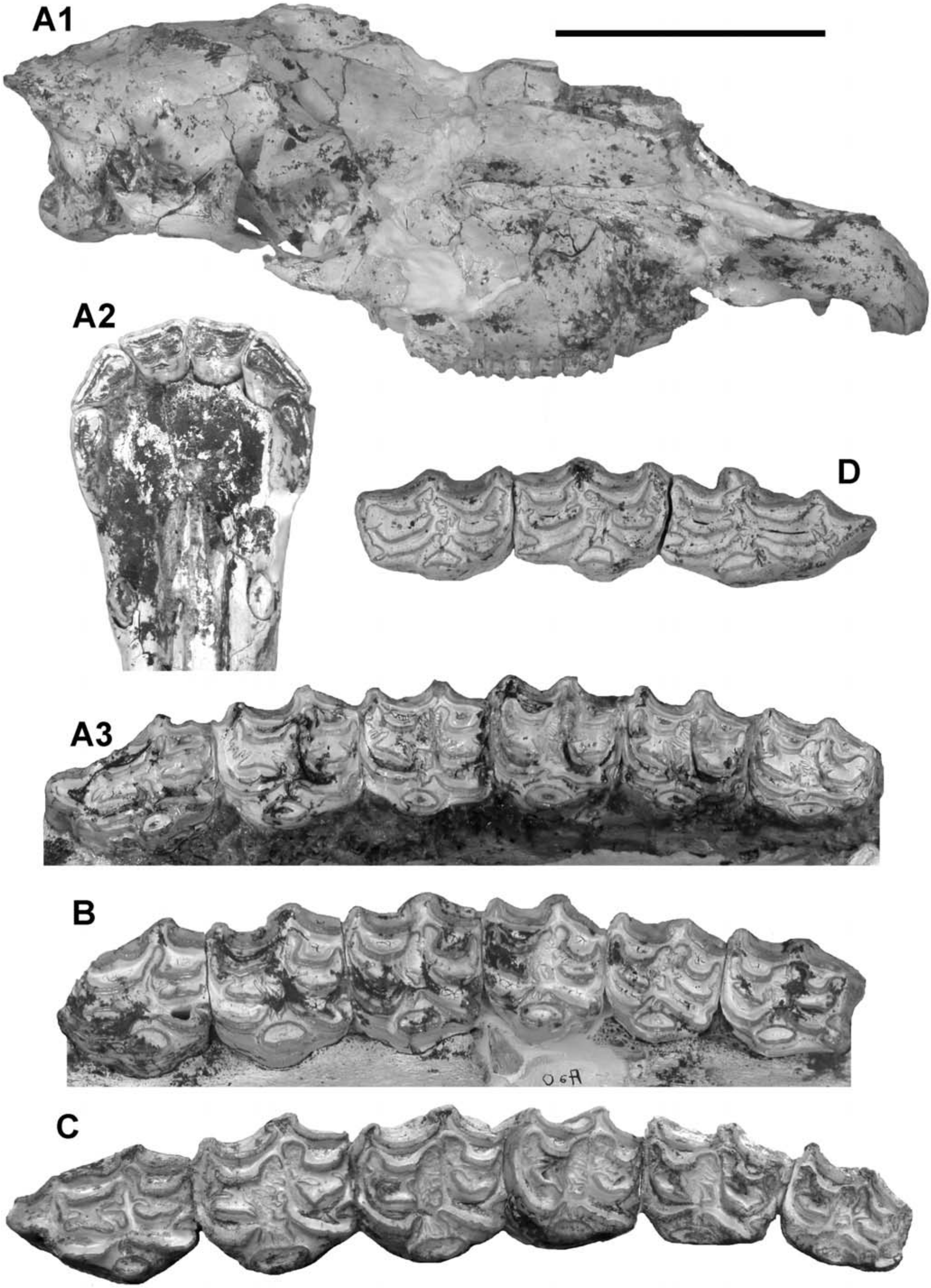

Figure 1. *Hipparion pomeli* sp. nov. from Ahl al Oughlam. **A**, holotype skull AaO-3647; **A1**, dorso-lateral view; **A2**, occlusal view of upper incisors; **A3**, cheek teeth; **B**, upper cheek teeth AaO-2048 (reversed from the right side); **C**, upper cheek teeth AaO-198 (M2 and M3 reversed from the right side); **D**, upper milk premolars AaO-4073. Scale bar = 15 cm for Fig. A1, 7.5 cm for Fig. A2, 5 cm and all others.

Table 1. Measurements in mm of hipparion skulls. *n*: number of specimens; approximate data in brackets.

		Oued el Hammam	LGB E	Chad	Hadar	Hadar	Hadar	AaO	Olduvai	Samos	Grebeniki	Taraklia	Villaroya	Kvabebi	Sor	Qiul, pers. comm.	Qiu *et al.* 1988	
		n = 1–9		KB	DD 2	KH 1–2	KH 2–3		BK II	*n* = 2–14	*n* = 1–4	*n* = 1–8	*n* = 2	K 48	PIN 3544	*H. houfenense*	*H. houfenense*	*H. huangheense*
		H. africanum	L22187	KB 9-AL 97-13	AL340-8	AL 164-3	AL 363-18	AAO 3647	2845/6	*H. dietrichi*	*H. giganteum*	*H. moldavicum*	*H. crusafonti*	*H.* cf. *crusafonti*	*H. garedz major*	THP 10508	THP 10733	FAM 11820
Muzzle length	1	125.5	125		140	>130		126	144	97.2	117	110.3	130	100	128	119	125	135
Palatal length	2	111	123	[140]	[135]	[155]	[126]	124	116	111.1	113.8	96	117	113	118	113	109	118
Vomerine length	3		113	135		[128]	[100]	112		94	109.5	104		103	[108]	[88]	[97]	
Postvomerine length	4		92			123,0	145	108		103.5	94	69				[122]	[108.7]	
Postpalatal length	5		198			[251]		220	[192]	183	216	178					200	250
Basilar length	6		452			>536		470		386	452.5	380				[431]	432	500
Premolar length	7	80.4		[85]	91	96	91	85		76.3	83.6	70.5	90	88	85–90	84	81	91
Molar length	8	67.8		82	75	76	73	77		64.8	67.5	59.8	73	71	69	67	38.5	80
Cheek teeth length	9	147.8	[152.1]	[173]	166	172	164	160	146.5	139.7	152	129.2	161	155	154	150	148	167
Choanal length	10		61	[74]			84	[52]		60.5	60.3	56.5	53		57			71
Minimal choanal width	11		[40]							31.8	36	30						31
Maximal choanal width	12	45.8	47	[43]			[47]			40	41	36		45	36			40
Palatal width	13	71.5	65	[90]			[80]			64.1	67.8	60.4		75	67			66
Minimal muzzle width	14	49	45		[31]	44		[35]		38.8	39.5	32.6	[40]	37	>33		[30]	42
Muzzle width at I3	15	59	57		57	60	80	60	70	63	58.9	42	[56]	52	[45]		[51]	66
Length of temporal fossa	16	71	78							71.3	85.5	69.8					82	82
Basion to foram. ethm.	17		135							162.3	157.5	122.5						
Frontal width	18	170	198				228	[190]		163.4	177	157		196		128		185
Bizygomatic width	19	180	192				221			163.6	180					136	[139]	188
Supraoccipital width	20		70		70		83	55				45					48	
Basioccipital width	21		92.5							95.3	99	88.5					92	110
Occipital height	22		71					65			75	61					71	
Anterior ocular line	23	352	363		400			390	360	300.8	343.8	300	365	320		334	320	380
Posterior ocular line	24		192		[190]		230	177		160	198.5	157				181	175	[205]
Facial height	25		118		102		110			82.3	87.2	91.3			102	98	90	112
Cranial height	26		106		[98]		[98]			80.9	92	75.8				109	96	
Height of auditive meatus	27		[10]								15.1							
Ant–post. orbital diameter	28	76	60				70	60		54	59.5	47.8	[62]	[51]		58	54	62
Vent–dors. orbital diameter	29		49			58	[54]	52		49.7	51.3	47.9	[45]			45	48	55
Length of naso-incisival notch	30	140.5	145		168			151	144	117.3	134.6	123.7	[150]		159	[154]	143	160
Cheek length	31	157	180	[130]	174		158	151	164	149	165	146.8	158			[156.8]	141	170
Orbit to preorbital fossa (POF)	32	46.5	40	43				50		44.9	48	26.9			34			
Length of POF	33	65,5	[55]	84						68.9	70	74.2			51			
POF to foramen infraorbitale	34	102 ?	–	90						50.4	56	76.7			62			
Height of POF	35	32	31	34						32.5	37.7	51.8			42			
POF to facial crest	36	52	[98]	47				66		39.7	39.7	25.3			27			
For. infraorb. to alveol. border	37	31	62	79						52.9	47	43.3			44		60	60
POF to alveolar border	38	58.5	–	113				[87]			54.5	67.3			63			
P2 - Orbit			182	207	196		192	175	168	143.2	169.5	148.3		166		[176.4]	[150]	185
Diastema					116			90										
Width of occipital condyles					74	81	85	>68										
Width of foramen magnum					33	38	39	[34]										

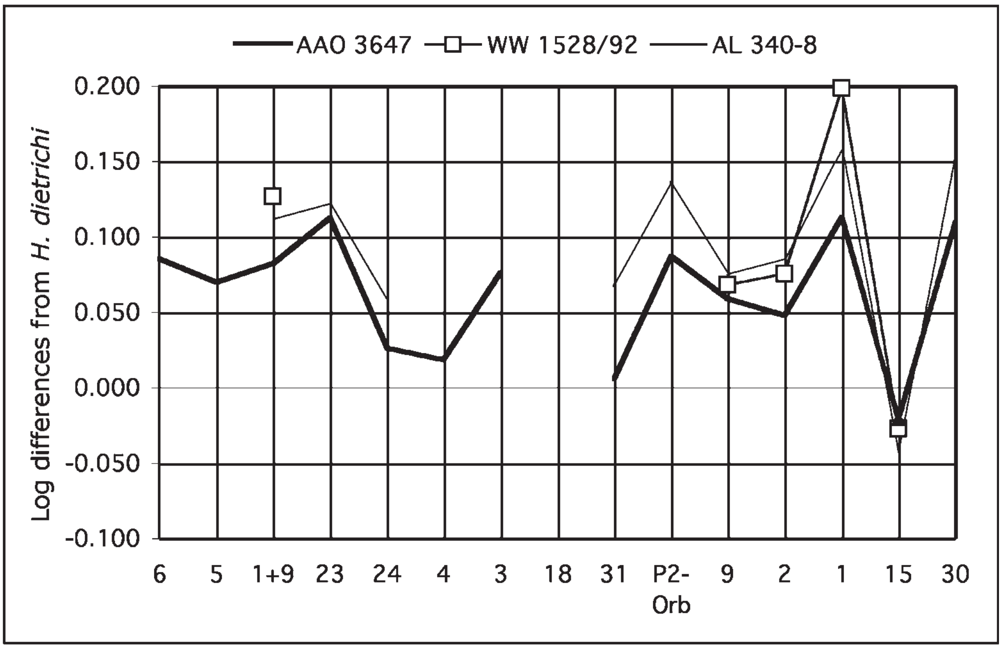

Figure 2. Ratio diagram comparing the holotype skull of *Hipparion pomeli* (AaO-3647) to *Hipparion hasumense s.l.* of Wembere Manonga Kilolei WW 1528/92 (data Bernor & Armour-Chelu 1997), and *H. hasumense* of Hadar DD AL 340-8. Data in Tables 1 & 2.

P3 and P4, the occlusal surface tends to be flat, while molars tend to have transversal ridges.

In Tunisia, the upper cheek teeth of Aïn Brimba are larger while those of Ichkeul are about the same size (Fig. 9; Tables 5 & 6). In East Africa, the more similar sizes may be found in the skull of *H. afarense* of the Kada Hadar and Sidi Hakoma members of Hadar, in Usno, and in member B of Shungura Formation. The Denen Dora teeth are often larger, while most of the Omo teeth are smaller.

A scatter diagram compares the hypsodonty of upper unworn or little worn M3s, plotting the height at the mesostyle versus length at mid-crown (Fig. 10). Schematically, three groups may be distinguished: less hypsodont in Chad (Kollé and Toros Menalla), Ichkeul; middle hypsodont ranging in time from Omo A (4–3.5 Ma) to Omo E (2.4–2.3 Ma); very hypsodont from Omo C (3–2.5 Ma) to Olduvai. Note that one of the two M3s of Omo C plots with middle hypsodont and the other with very hypsodont, indicating the possible presence of two species. The little worn M3 of AaO appears moderately hypsodont. The Hypsodonty Index (HI = mesostyle height × 100/length at mid-crown) is 221–235 in the less hypsodont group, 241–276 in the middle hypsodont, and 297–315 in the very hypsodont one.

Three groups appear again for unworn or little worn other upper cheek teeth (Fig. 11). A very hypsodont group (HI = 318–340) comprises teeth from Olduvai, KBS, Omo F, Omo G, but also, surprisingly, one tooth from Omo B.

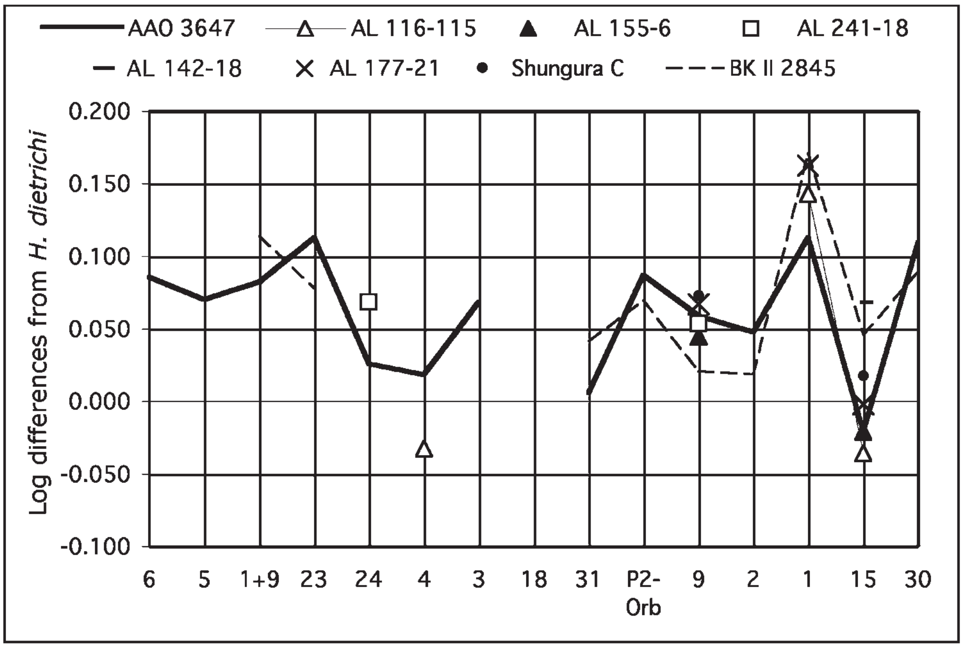

Figure 3. Ratio diagram comparing the Moroccan skull (AaO 3647) to *Hipparion hasumense s.l.* of Hadar SH (AL 142-18), DD (AL 116-115, AL 155-6, AL 241-18, AL 177-21), Shungura C (18-1968-363 and 18-1969-90), and Olduvai BK II 2845/6. Data in Table 2.

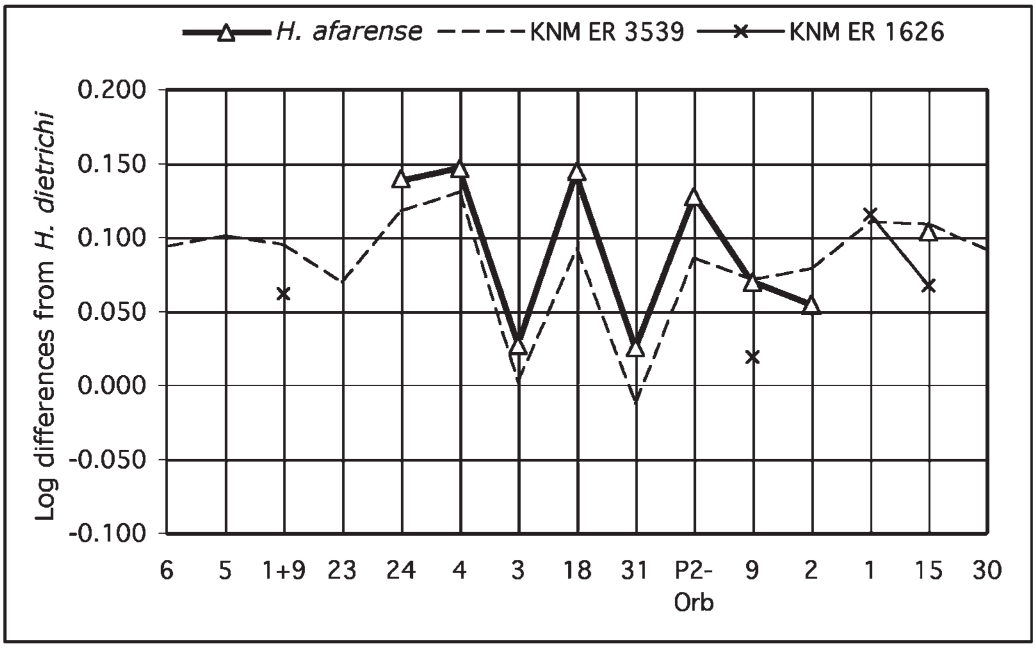

Figure 4. Ratio diagram illustrating the pattern of *Hipparion afarense* type skull and *H. afarense s.l.* from East Turkana Burgi (KNM ER 3539) and *Notochoerus scotti* Zone (KNM ER 1626). Data in Table 1, Appendix Table 2, and Appendix Text.

The middle hypsodont group (HI = 264–298) comprises specimens from Hadar DD and unknown levels, Omo C, Omo F, and Kossom Bougoudi, Chad. Aïn Brimba and Ichkeul plot with the less hypsodont group (HI = 243–257). Again, there is possible evidence for two species at the same time: at Hadar DD2, Omo F, and at Chad Kossom Bougoudi. There are no data for AaO.

Deciduous upper cheek teeth. They are moderately plicated but with large or bifid plis caballins (Fig. 1D). Data are provided in Table 7.

Permanent lower cheek teeth. Four individuals are represented by complete series (Fig. 8A,B; Table 8). There are also 12, mostly isolated, specimens (Table 9). The teeth are caballoid, with protostylids (plis or isolated) and ectostylids. Most ectostylids are not very large, although they are larger at the base of the crown. In two molars there are additional ectostylids, very small but reaching the occlusal surface at least *c.* 3 cm from the roots. The caballoid pattern of the lower cheek teeth indicates without any doubt that the AaO hipparion is an 'advanced' hipparion. What additional indications may be gathered from the presence of ectostylids ?

The development of ectostylids and their possible use for biostratigraphy has been discussed in detail for samples from Hadar, Omo, and East Turkana (Eisenmann 1977). Although there are no extensive analyses of the function of ectostylids, it seems likely that they do have some function, possibly in increasing grinding ability. It is

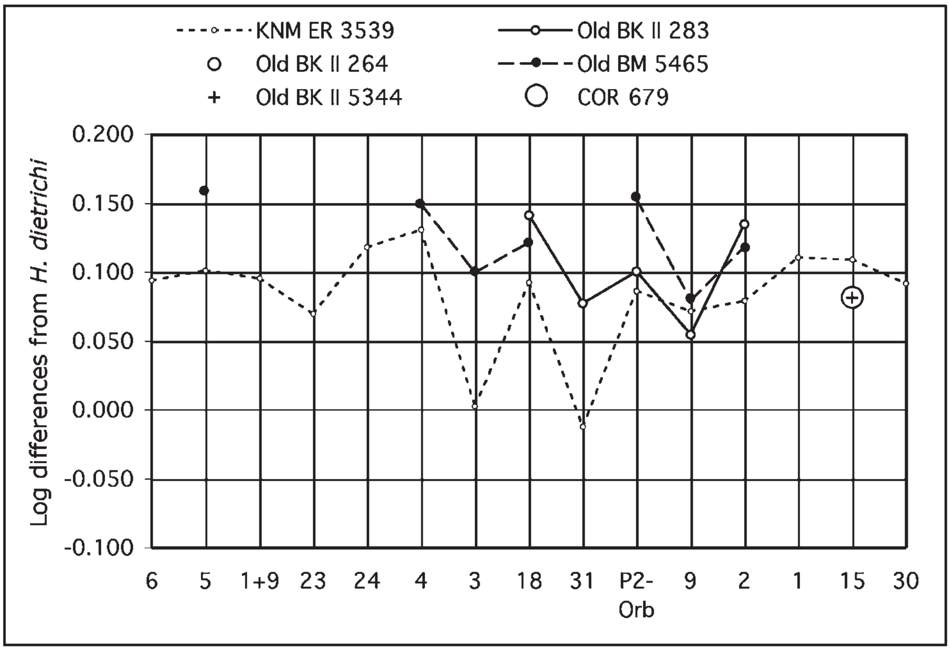

Figure 5. Ratio diagram illustrating the pattern of other *Hipparion afarense s.l.* skulls from Olduvai Bed II (BK II 264, 283, 5344) and unknown (BM 5465), and Cornelia. Data in Table 2, Appendix Table 2, and Appendix Text.

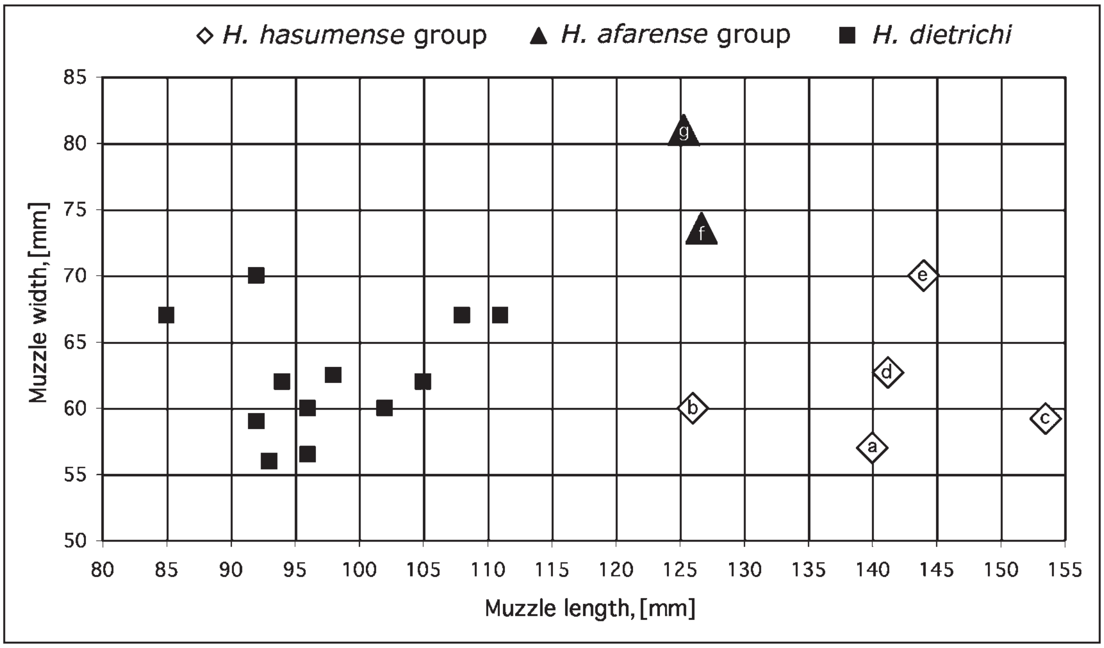

Figure 6. Scatter diagram of muzzle lengths and widths in *Hipparion dietrichi* of Samos (Table 2), *H. hasumense s.l.* a: AL 340-8, Hadar DD; b: AaO 3647, Ahl al Oughlam; c: WW 1528/92, Wembere Manonga, Kilolei; d: AL 177-21, Hadar DD; e: Olduvai BK II 2845/6; and *H. cornelianum* f: KNM ER 1626, East Turkana *Notochoerus scotti* zone; g: KNM ER 3539, East Turkana Burgi.

clear, however, that whatever their function, as long as ectostylids are not yet in wear, the plis caballinid appear as some kind of 'vicariants' of ectostylids, providing occlusal enamel at the very position occupied later by ectostylids. A good illustration is provided by the molar Omo C 40-68-3015 (Eisenmann 1985, plate 2-17-18) and by several teeth from Aïn Brimba (Arambourg 1970, plate XVII-11,11a):

— On the occlusal surface of a little-worn m2, the pli caballinid is very well developed; the apex of a first ectostylid appears 12 mm below the occlusal surface; the apex of a second ectostylid is visible 10 mm below the first; at that level, the first ectostylid is about 5 mm long; a few millimetres below, the second ectostylid is nearly as long as the first; if they were to fuse, the total ectostylid length would be about 8–9 mm.

— On the slightly more worn m1 of the same series, the first ectostylid is already beginning to wear, taking the place of the nearly absent pli caballinid; the apex of the second ectostylid is visible 32 mm below the occlusal surface.

— On the unerupted p4, an ectostylid appears *c.* 10 mm below the occlusal surface; between the occlusal surface and the ectostylid there is a well-developed pli caballinid.

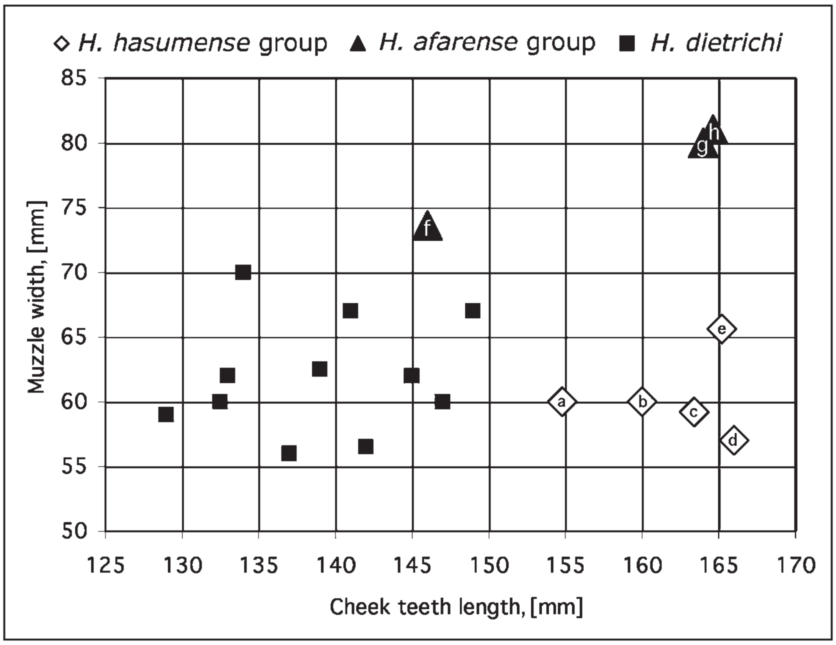

Figure 7. Scatter diagram of P2-M3 lengths and muzzle widths in *Hipparion dietrichi* of Samos (Table 2), *H. hasumense s.l.* a: AL 155-6, Hadar DD; b: AaO 3647, Ahl al Oughlam; c: WW 1528/92, Wembere Manonga, Kilolei; d: AL 340-8, Hadar DD; e: 18-198-363 & 18-1969-90, Omo C; and *H. afarense s.l.* f: KNM ER 1626, East Turkana *Notochoerus scotti* zone; g: AL 363-18, Hadar KH; h: KNM ER 3539, East Turkana Burgi.

Table 2. Measurements in mm of hipparion skulls. Numbers refer to the measurements defined in Table 1. Approximate data in brackets. Asterisks indicate skull estimations from mandibular data (see Appendix). Data for Manonga WW 1528/92 are according to Bernor & Armour-Chelu (1997).

	1	4	3	9	15	23	24
H. hasumense s.l.							
Hadar AL 116-115	[135]	[96]			58		
Hadar AL 155-6				154.8	60		
Hadar AL 177-21	141.2*				62.7*		
Hadar AL 241-18				[158]			[195]
Shungura C 18.1968.363				165.2	65.6*		
Manonga WW 1528/92	153.5			163.4	59.2		
Olduvai BK II 2846	144			163.5	[70]	[360]	
H. afarense s.l.							
AL 142-18					74		
Shungura F 118-1972-5				142			
KNM ER 1626	126.7*			146	73.6*		
Olduvai BK II 264					76		
Olduvai BK II 067-5344					75.8*		
Cornelia COR 707					74*		
H. dietrichi							
Münster SI 7	93			137	56	290	
FAM Q1 no number	111				67		
FAM Q1 20559 A	91			148		295	
FAM Q1 20596	85	97	92	149	67	300	155
FAM Q1 20598	92		106		70	310	
FAM Q1 20608	102			147	60	305	
FAM Q1 20692				134	70		
FAM Q1 20997	94		94	145	62	310	
FAM Q1 94907				140			
FAM Q4 22860	108	110	91	141	67	325	
FAM Q6 22990	96			142	56.5	305	165
Darmstadt 1914	98			139	62.5		
Chicago 12868	96		87	132.5	60	294	
Bern 45	92			129	59	280	
Bern 109	105			133	62	295	
H. crassum s.l.							
Pp 208 mandible	154.5*			177	61.2*		
Chamar 3381-53.	146.8*			176	63.4*		

Measurements of Aïn Brimba lower cheek teeth are given in Table 10.

At Ichkeul, the apex of the ectostylid on an unworn premolar is about 9 mm from the occlusal surface. The tooth was sectioned at 2 cm from the occlusal surface. At this level, the length is 28 mm, the width is 14.7 mm, the double knot is 14.7 mm long, the postfossette 12.2, the ectostylid 3 mm. The rest of the tooth is broken.

The growth of teeth proceeding from apex to roots, the distance between the apex of the tooth and the apex of the ectostylid(s) should be more meaningful in terms of evolution than the height of the ectostylid from the base of the crown. In the Omo C5-8 little worn m2 (Eisenmann 1985, plate 2-18) the first ectostylid appears more 'evolved' – i.e. closer to the occlusal surface, than in the m2 of Aïn Brimba while in an unworn p4 of the Kilolei Member of Wembere-Manonga Valley (Bernor & Armour-Chelu 1997), the distance is the same as in the p4 of Aïn Brimba. Naturally in different species the development of ectostylids may be different: from the Ibole Member of Wembere-Manonga Valley (Bernor & Armour-Chelu 1997), the ectostylid of one m2 (large species) is at more than 37.6 mm from the occlusal surface, while in another m2 (small species), the distance is only 13 mm. But in the m2 of the large species of Kilolei member, the ectostylid has grown to less than 13.9 mm from the occlusal surface.

In Omo member F, the first ectostylid at least is already formed at the apex of the crown (Eisenmann 1985, plate 2-5). Three or even four ectostylids appear on sectioned teeth from Omo G (Eisenmann 1985, plate 2-9). Their fusion results in a peculiar, inflated and trifid ectostylid, at times almost fused with the pli caballinid (Eisenmann 1985, plate 2-12-15). This seems to be the ultimate degree of ectostylid evolution. A trifid pattern is already present in some teeth of the Denen Dora member of Hadar (AL 183-41). It may also be seen at Koobi Fora (KNM ER 2766 SU-, Burgi and KBS).

At AaO, there are no unworn lower p3–m2 so we do not know if ectostylids had already developed at the apex of the crown. There is no evidence of the peculiar trifid pattern of Omo G; the ectostylids are not very large but a second ectostylid may occur (AaO-4072). In East Africa, the pattern would be consistent with an age older than 3 Ma.

Deciduous lower cheek teeth. Most teeth are in the very first stages of wear (Fig. 8C; Table 11). Protostylids are always present and may sometimes be isolated. Ectostylids are not very large. They appear about 10 mm below the top of the tooth. Secondary ectostylids appear about 5 mm lower. It may be noted that the double knots of dp2 grow

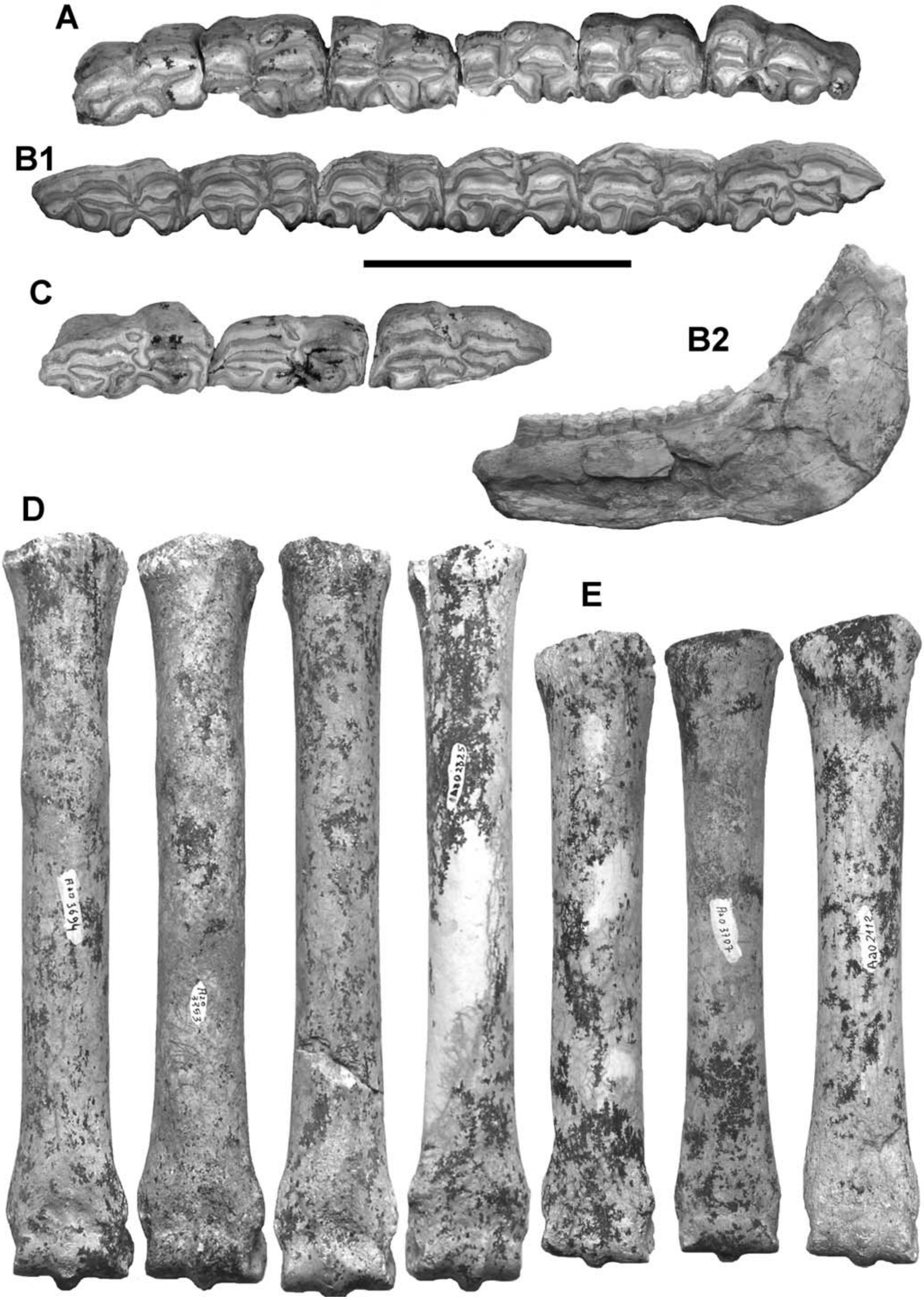

Figure 8. *Hipparion pomeli* sp. nov. from Ahl al Oughlam. **A**, lower cheek teeth AaO-2993. B: mandible AaO-197; **B1**, cheek teeth, **B2**, lateral view. **C**, lower milk premolars AaO-4070. **D**, four metatarsals, from left to right: AaO-3694, AaO-3353; AaO-3700, AaO-2825. **E**, three metacarpals, AaO-4267, AaO-3307, AaO-2112. Scale bar = 20 cm for Fig. 2; 10 cm for Figs D–E; 5 cm for all others.

Table 3. Permanent upper cheek series or associated teeth from Ahl al Oughlam. Measurements in mm, approximate values in brackets.

AaO 198		P2	P3	P4	M1	M2	M3
Wear stage		2	2	2	2	2	2
Length	Occlusal	35.5	29	27	26	25	24
Width	Occlusal	24	28	28	25	24	19.5
Protocone L	Occlusal	8	11	10.5	9.5	9	9
Protocone W	Occlusal	5	4.9	4.7	4.3	4.3	4
Plis fossette		5	12	13	12	13	8
Plis caballin		1	3	3	3	2	3

AaO 1452		P2	P3	P4	M1		
Wear stage		2	2	2	2		
Height		37	[30]	[38]			
Length	Occlusal	35	29.5	27	[24]		
Width	Occlusal	25	27	25	25		
Protocone L	Occlusal	7.3	10.7	8.8	8.5		
Protocone W	Occlusal	4	4	4.1	3.9		
Plis fossette		9	15		[16]		
Plis caballin		1	3	1	2		

AaO 2048		P2	P3	P4	M1	M2	M3
Wear stage		2–3	2–3	2–3	2–3	2–3	2–3
Height					42	40	30
Length	Occlusal	[31]	25	24	21.5	21	23
Width	Occlusal	24	25.5	26	24.1	22	20
Protocone L	Occlusal	8	9	8.5	8.5	8	8
Protocone W	Occlusal	5	5	4.9	4.7	4	3.9
Plis fossette		7	9	>8	12	13	12
Plis caballin			2	2	1	1	1

AaO 3495		P2	P3	P4	M1	M2	
Wear stage		2	2	2	2	2	
Height		40	52	57	52	57	
Length	Occlusal	36	28	28	25	26	
Width	Occlusal	26	28	27.2	25	23	
Protocone L	Occlusal	9.2	10	9	8	8.5	
Protocone W	Occlusal	4.2	4.3	4.2	4	4	
Length	at 2 cm	35	27	26	24	24	
Width	at 2 cm	24.7	27	26.7	26	24	
Length	at 1 cm	34	25	24.2	22.1	23	
Width	at 1 cm	24	26.2	27	26	24	
Plis fossette		12	17	16	18	14	
Plis caballin		1	1	2	2	2	

AaO 3647		P2	P3	P4	M1	M2	M3
Wear stage		2	2	2	2	2	2
Length	Occlusal	33.5	27.5	25	24	23.5	24
Width	Occlusal	24	26	25	25	24.5	20
Protocone L	Occlusal	7	8.5	7	9	9	7
Protocone W	Occlusal	4	4.9	4	4	4.1	3
Plis fossette		9	16	24	16	16	11
Plis caballin		2	1	1	1	1	1

		AaO 1429a P2	AaO 1429b P3		AaO 1431 M1	AaO 1432 M2	AaO 1433 M3
Wear stage		2–3	2–3		2	2	1–2
Height		42	46		53	59	61
Length	Occlusal		29		25	26	22
Width	Occlusal	24.5	27		24	24	18
Protocone L	Occlusal	8	8		9	8.3	9
Protocone W	Occlusal	4.4	4.2		4	4.5	3.6
Length	at 2 cm		28		24	24	24
Width	at 2 cm	24.7	25		24	24	21.5
Length	at 1 cm		26		23	23	25
Width	at 1 cm	23	25		25.2	23	21

Continued on p. 61

Table 3 (*continued*)

		AaO 1429a P2	AaO 1429b P3		AaO 1431 M1	AaO 1432 M2	AaO 1433 M3
Plis fossette		12	22		22	24	
Plis caballin		1	4		2	1	
		AaO 3937a P4	AaO 3937b M1	AaO 3937c M2		AaO 3167 M1	AaO 3167 M2
Wear stage		3	3	3		4	4
Height		[30]	[30]	33		17	
Length	Occlusal	24	23	22.2		23	23.2
Width	Occlusal	25.1	25.2	23.2		27.2 sic	23
Length	at 1 cm	24	23	22.5			
Width	at 1 cm	26	25	24			
Protocone L	Occlusal	8	8.2	8		9.8	10
Protocone W	Occlusal	5	4.5	4		6	6
Plis fossette		[16]	19			10	10
Plis caballin		1	1	0			

in the same way as the ectostylids, i.e. by fusion with a secondary enamel pillar a few millimetres below the top of the crown.

Size index, variability of limb bones, and sexual dimorphism. Obviously, the size of a specimen can be qualified by comparisons with the same kind of specimens. But how can the size of a talus be compared with the size of a second phalanx? And how can we determine if the overall size of animals found at one locality was larger or smaller than at another? The Variability Size Index (VSI) is a way

Table 4. Other permanent upper cheek teeth from Ahl al Oughlam. Asterisks for dimensions at mid-crown height.

		AaO 3551 P2	AaO 3599 P2	AaO 1229 P2	AaO 2263 P2	AaO 4071a P	AaO 4071b M	AaO 37 M	AaO 1179 M?
Wear stage		2–3	2–3	2–3		[3]			
Height		32	33						
Length	Occlusal		33	32	35.8	24.7	22	23	24
Width	Occlusal	24	24	23	24.7	28 sic	24	25	23
Protocone L	Occlusal	8	8	7.8	7.9	10	9	9	8
Protocone W	Occlusal	3.6	4	4.1		5	5	5	4
Plis fossette		9	6	5		8	11	[14]	
Plis caballin		1	1	1		2			2
		AaO 1475 P	AaO 3132 P	AaO 3130 M	AaO 3555 M	AaO 1438 M			
Wear stage		2	2–3	2	2	3			
Height		42	40	44	46	21			
Length	Occlusal	26	25.1	25	25	21.6 sic			
Width	Occlusal	25	25	23	23	21.1 sic			
Length	at 2 cm	25	24	23	23.7	21.6 sic			
Width	at 2 cm	25.3	25.2	23	23	21.1 sic			
Length	at 1 cm	25	23	23		21 sic			
Width	at 1 cm	25	25	23	22	22 sic			
Protocone L	Occlusal	8	8.1	8	8	8			
Protocone W	Occlusal	4	4.1	4.2	3	4			
Plis fossette		12	20	8	14	11			
Plis caballin		2	1		1	1			
		AaO 1440 M3	AaO 3134 M3	AaO 3133 M3	AaO 3556 M3	AaO 3557 M3	AaO 3598 M3	AaO 4071c M3	AaO 4071d M3
Wear stage		0	0	1–2	1–2	2	4	3	4
Height				45	45	47	19		
Length	Occlusal						25		25
Width	Occlusal						23		22.5
Length	Mid-crown	23	23	24.5	24.5	25.1		24	
Width	Mid-crown	20	19.5	21	21	22.3		21	
Protocone L	Occlusal	7*	7.4*	9	8.2	9.1	10.1	8	11
Protocone W	Occlusal			3.2	3	3.2	4	4	4.5
Plis fossette				[9]	8	12	11	11	8
Plis caballin				1	2	3	2	1	[2]

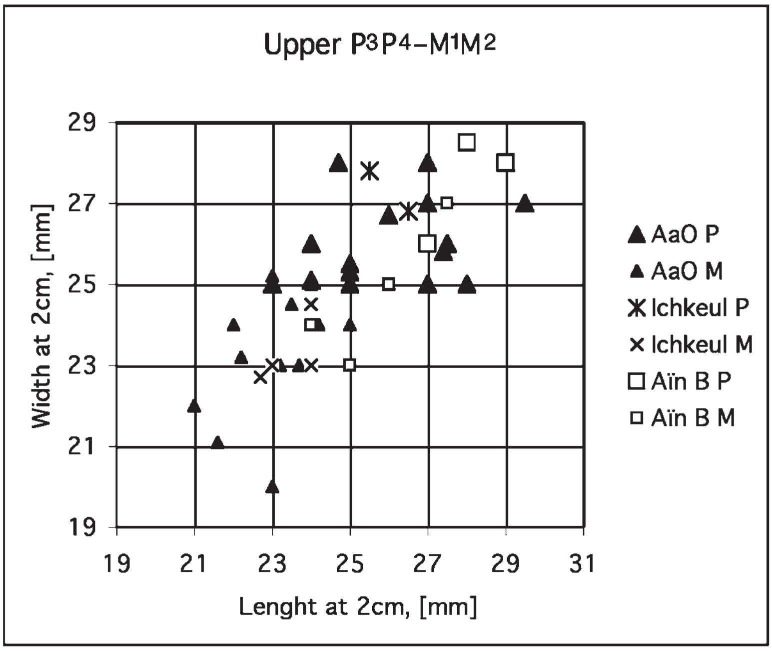

Figure 9. Scatter diagram of P3-4 and M1-2 lengths and widths of Ahl al Oughlam, Ichkeul, and Aïn Brimba.

Table 5. Permanent upper cheek teeth from Aïn Brimba.

		1958.14.173 P2	1958.14.221 P3	1958.14.187 P4	1958.14.190 P4	1958.14.190 P4	1957.111.13 P?	
Wear stage		0–1	2	1	0–1	section	2–3	
Height		56	33	61	67	41	43	
Length	Occlusal	40	29	29	32	30.2	[25]	
Width	Occlusal	24	28	27	27	29		
Length	at 2 cm	38	29	27		28		
Width	at 2 cm	25.6	28	26		28.5		
Length	at 1 cm	39	28	26.5		27.5		
Width	at 1 cm	24.6	27	27		28.5		
Protocone L	Occlusal	[10]	10	9.9		7.9	7	
Protocone W	Occlusal		5	3.8		5	4	
Plis fossette			21	22		23	19	
Plis caballin			2	2		1	3	
		1958.14.222 M?	1958.14.191 M1	1958.14.191 M1	1958.14.172 M	1958.14.186 M	1958.14.188 M	1958.14.189 M
Wear stage		2–3	0	section	2	1–2	1–2	2
Height		37	[72]	30	52	60	60	56
Length	Occlusal	26	29	28.5	27	27	26	26
Width	Occlusal	[26]	27	28		[26]		
Length	at 2 cm	27		27.5	25	24	25	26
Width	at 2 cm			27		26		
Length	at 1 cm	27		26	24	24	23	25
Width	at 1 cm			27.5		26		
Protocone L	Occlusal	[10]		7.3		9		
Protocone W	Occlusal			5		4		
Plis fossette		25		20	20	21		[20]
Plis caballin		4		3		1		
		1958.14.223 M3	1958.14.192 M3					
Wear stage		2	1–2					
Height		38	55					
Length	at midcrown	28						
Width	at midcrown	23						
Protocone L	Occlusal	10	9					
Protocone W	Occlusal	3	3.9					
Plis Fossette		22	[13]					
Plis Caballin		2	1					

Table 6. Permanent upper cheek teeth from Ichkeul.

		1950.1.123 P3	1950.1.104 P4
Wear stage		2	1–2
Height			55
Length	Occlusal	26.5	27
Width	Occlusal	26.8	25.6
Length	at 2 cm		25.5
Width	at 2 cm		27.8
Length	at 1 cm		25.1
Width	at 1 cm		28
Protocone L	Occlusal	7	11
Protocone W	Occlusal	4.8	4
Plis fossette		19	
Plis caballin		2	2

		1948.1.8 M1	1948.1.8 M1	1950.1.21 M2	1950.1.21 M2	1948.2.15 M2	1950.1.107 M2	1948.2.14 M	M
Wear stage		1	section	1–2	section	1	1–2	[2]	section
Height		59	28.5	61	41	59	55	[55]	27
Length	Occlusal	24	24	26	25.5	25	25		
Width	Occlusal	21.5	23	22.5	25	19	20.2		[22]
Length	at 2 cm			27.5	24	23	[23]		
Width	at 2 cm				24.5	22.7	[23]		
Length	at 1 cm		22.5		24	22.7			
Width	at 1 cm		22		24	23			
Protocone L	Occlusal	8	8	8	7.1	7	8.1		7
Protocone W	Occlusal	3	4.2	3	4	3	3.9		4
Plis fossette			16		21		13	[20]	>10
Plis caballin			1	1		0	2		1

		1949.1.9 M3	1949.1.9 M3
Wear stage		0	section
Height		56	27
Length	at midcrown	25	25
Width	at midcrown	23	22
Protocone L	Occlusal	10	9
Protocone W	Occlusal	3	4
Plis fossette		22	16
Plis caballin		2	3

to address these questions. Devised by archeozoologists (Uerpmann 1982; Meadow 1999), the VSI is one of the size index scaling techniques available. A sample including all the bones of a taxon is chosen as reference. Mean and standard deviation are calculated for each measurement of the sample. Comparisons are carried out using the following formula: VSI (variability size index) = $25(x–m)/s$ where s is the standard deviation of the mean (m) of the reference measurements to which another measurement (x) is being compared. The obtained values are plotted on a histogram graduated in one, two, three, or more standard deviations from the reference. As phrased by Meadow (1986), 'Using this formula, the standard dimension is set at zero; a measurement one standard deviation larger than the standard (reference) dimension will be plotted at 25, one standard deviation smaller at –25, etc'. It is recommended to use the same kinds of dimensions (widths, or depths, or lengths) for all the bones. In this study we have tried to ascertain if this technique can provide some interesting information.

1. VSI based on Höwenegg sample. The detailed description by Bernor *et al.* (1997) of the late Miocene Höwenegg sample affords the first basis of normal intraspecific variation for hipparions. Among the published measurements we have chosen to use only widths (Table 12), because they are more frequently available on fossils than lengths and depths, and because it is not recommended to combine different kinds of measurements. For the tibial diaphysis width, we have used the median of Höwenegg (44.6) instead of the mean (42.6) and we supposed a standard deviation of 2 instead of 5.61 because they appear more consistent with the rest of the data: a minimal value of 32.4 and a corresponding standard deviation of 5.61 indicate either the inclusion of a juvenile specimen or a printing error; there is no reason why the standard variation would be more than 5 for the tibia width when it comprises between 1.1 and 2.66 for other bone widths.

Equus bones do not exhibit sexual dimorphism, at least not in a marked way. There is no evidence yet that it was otherwise in hipparions (Bernor *et al.* 1997). The distribution of metrical values within a monospecific adult (epiphyses

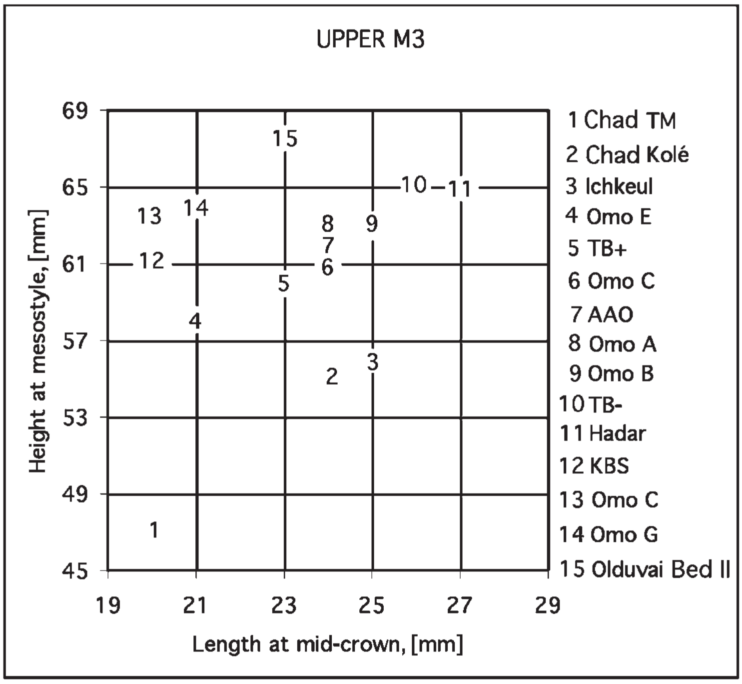

Figure 10. Scatter diagram of unworn or little worn M3 lengths and heights in various African hipparions. HI: Hypsodonty Index. 1: TM 47-101-11; HI = 220.8; 2: KL 20-98-11, HI = 235; 3: Ichkeul, HI = 224; 4: 1968-1005-38, HI = 276.2; 5: 4094, FS 751, HI = 260.9; 6: L 768-1, HI = 254.2; 7: AaO 1433, HI = 258.3; 8: 1969-108-81, HI = 262.5; 9: L 1-61, HI = 252; 10: ER 2922, HI = 250; 11: AL 58-10, HI = 240.7; 12: ER 1263, HI = 305; 13: L 724-3, HI = 315; 14: L 675-2, HI = 304.8; 15: average of Hooijer (1975), HI = 296.7.

perfectly fused) sample should be normal. In consequence, an 'abnormal' variation or distribution may reflect a long time of deposition during which a given species could have changed, or the coexistence of different taxa, or sexual dimorphism.

The AaO histogram seems, on the whole, to follow a normal distribution, centred on a peak between 50 and 75, i.e. at two to three standard deviations from Höwenegg (Fig. 12). But eight values plot between 175 and 250, evidencing the presence of surprising widths. All of them

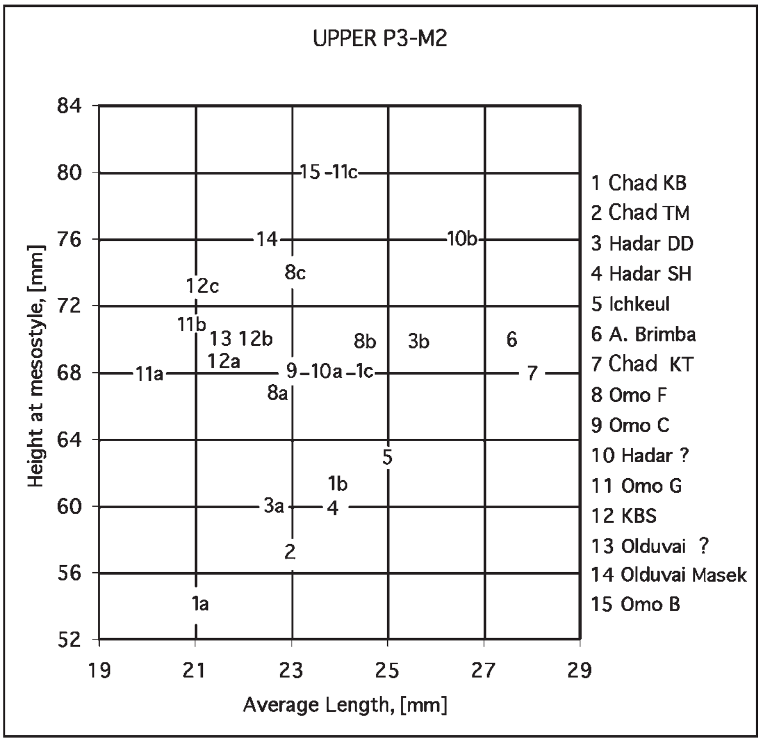

Figure 11. Scatter diagram of unworn or little-worn P3-4 and M1-2 lengths and heights in various African hipparions. HI: Hypsodonty Index. 1a: KB3 98-93, HI = 257.1; 1b: KB4 96-13, HI = 254.2; 1c: KB3 97-136, HI = 277.6; 2: TM 47 101-1C, HI = 247.8; 3a: AL 155-6, HI = 264.3; 3b: AL 305-5, HI = 274.5; 4: AL 58-10E, HI = 251; 5: 1950–1-21, HI = 252; 6: 1958-14-191, HI = 254.5; 7: KT33 96-1, HI = 242.9: 8a: L 253-3a, HI = 297.8; 8b: 1972-14-108, HI = 285.7; 8c: L 398-1182, HI = 321.7; 9: L 767-1, HI = 295.7; 10a: AL 239-68, HI = 285.7; 10b: AL 288-19, HI = 286.8; 11a: F 513-33, HI = 340; 11b: L 616-62, HI = 338.1; 11c: L 627-89, HI = 333.3; 12a: ER 2263, HI = 320.9; 12b: ER 2073, HI = 318.2; 12c: ER 1231, HI = 347.6; 13: A 581, HI = 325.6; 14: 1692, HI = 337.8; 15: 1973-1958-212, HI = 340.4.

Table 7. Deciduous upper cheek teeth from Ahl al Oughlam.

		AaO 4073 dP2	AaO 4073 dP3	AaO 4073 dP4	AaO 3600 dP2	AaO 3600 dP3	AaO 1447 dP4
Wear stage		2	2	2	0–1	0–1	0–1
Height		*c.* 20	*c.* 20	*c.* 20	23	26	26
Length	Occlusal	38.0	29	29	>37	30	32
Width	Occlusal	20	21	19	*c.* 20	*c.* 20	19
Protocone L	Occlusal	8	7	7.7	9.5	10	9
Protocone W	Occlusal	*c.* 3	*c.* 3	*c.* 3			
Plis fossette		[8]	14	10			
Plis caballin		1	2	1			

		AaO 1186 dP2	AaO 3552 dP3	AaO 3546 dP4	AaO 1439 dP3	AaO 1437 dP4
Wear stage		2	2	2	0–1	0–1
Height			18	20.5	24	25
Length	Occlusal	38.0	28	29	29	30
Width	Occlusal	19	19	19.5	18	19
Protocone L	Occlusal	6	6.5	7	*c.* 8	7
Protocone W	Occlusal	*c.* 3	*c.* 2	*c.* 3		
Plis fossette		[10]	12	13		
Plis caballin		1	1	2		

		AaO 1466 dP3–4	AaO 3537 dP3–4	AaO 3538 dP3–4	AaO 3539 dP3–4
Wear stage		0–1	0–1	0–1	0–1
Height		28	26	24	25
Length	Occlusal	32.0	29	31	31
Width	Occlusal	20	19	21	22
Protocone L	Occlusal	10	8.5	9	10

are proximal widths of MC III. The preserved six distal widths of the corresponding MC III plot between 50 and 150. Thus, the asymmetry of the histogram reflects only an anatomical difference between AaO and Höwenegg MC III: in the first, the proximal epiphyses of some MC III are relatively wider.

According to the coefficients of variation, the variability of AaO is compatible with the variability of some assumed monospecific samples of *Equus,* but compared to the best samples of *Equus* (Eisenmann & David 2002; Eisenmann 2002, 2004), and *Allohippus,* the size variability at AaO is greater. Indeed, the coefficients of variation of the tali are quite bigger than in the well-represented extant *Equus grevyi* and bigger too than in the very large fossil sample of *Allohippus vireti* from Saint-Vallier (Table 13). Since the fossils of AaO are believed to have been deposited during a short period (see Introduction), and since there is no evidence for the coexistence of two species, we cannot exclude that some sexual dimorphism existed in *H. pomeli,* but this does not appear clearly on the VSI histograms.

Although much poorer than AaO's, the Hadar DD sample is interesting because it includes a nearly complete skeleton: AL 155-6. In Fig. 12, it is represented by white points. One of the largest values of AL 155-6 is, as in *H. pomeli,* the proximal MC III width (the two others are second and third phalanges widths). On the larger side of AL 155-6 plot two radii (AL 155-1 and 338-13), one distal MC III (AL 155-1), one proximal MC III (AL 116-33), and one second phalanx (Al 340–1). After consideration of the other dimensions (not included in our VSI), it appears that only the fragmentary MC III AL 155-1 (extreme point in Fig. 12) belongs without any doubt to a larger hipparion.

The recurring very large deviations of MC III proximal widths from the Höwenegg standard suggests that this old hipparion is not quite appropriate as a basis for size comparison for much younger hipparions. We have therefore tried to use *H. pomeli* as standard for further size comparisons.

2. VSI based on *H. pomeli* sample.

Using this reference (Table 12), the AaO histogram is of course 'normal' (Fig. 13). The Koobi Fora hipparions are somewhat smaller: the white ellipses indicate KBS member specimens, the two black squares correspond to tali from Chari and 'TB-?'. The Olduvai Bed II sample appears to possibly include two species: a distal MC III (DC II 52/679) seems very large.

Figure 14 shows the size differences between members A–B and G of the Omo Shungura sequence: a very small hipparion appears in member F, possibly represented later in the KBS member of the Koobi Fora Formation.

Hipparions of Hadar (Fig. 15) appear somewhat larger than those of Shungura (Fig. 14). At DD, there is an impression of three size groups, the associated bones of AL 155-6 plotting with the smallest. Using AaO as standard instead of Höwenegg (Fig. 12), AL 155-6 acquires a normal distribution. The presence of an extremely large hipparion (AL 155-1) is confirmed.

Table 8. Permanent lower cheek series or associated teeth from Ahl al Oughlam. Measurements in mm, approximate in brackets. L: length. W: width.

AaO 3180	P2	P3	P4	M1	M2	M3
Wear stage	3	3	3	3	3	3
Height	–	–	–	–	–	20
L occlusal	31.5	26	26	–	23.6	–
Ante fossette	–	9	9	7	7	8.1
Double knot	14	[17]	–	–	15.1	15.1
Post fossette	10.1	12.7	11.7	8	10	10
W occlusal	15	[16]	–	–	14	12.7
L ectostylid	3	8.1	7	+	7 & 1	4 & 1
W ectostylid	2.5	4.1	4	+	3	2.7
Protostylid	0	pli	pli	pli	pli	pli
Pli caballinid	0	0	0	–	#	0
AaO 197	P2	P3	P4	M1	M2	M3
Wear stage	1–2	1–2	1–2	1–2	1–2	1–2
L occlusal	32	25.9	25	24	24	28
Ante fossette	10	9.7	9	7.5	8	8.3
Double knot	13	16	16	15	14	12.2
Post fossette	12.7	12	12.2	10.1	10.3	10
W occlusal	12	14.2	14.5	13.5	14	13
L ectostylid	2.0	8.0	7.0	6.0	5.5 & 1	1.5
W ectostylid	1.5	4.1	4	4	3 & 1.5	2
Protostylid	0	0	0	0	0	0
Pli caballinid	0	+	0	+	0	0
AaO 1182	P2	P3	P4	M1	M2	M3
Wear stage	1	1	1	1	1	1
Height	42		61.5	52.5		60.5
L occlusal	30	27	26.1	25	24	25
Ante fossette	9	10	9	7	8.9	7.8
Double knot	13	16.1	15	15	14.5	11.5
Post fossette	14 sic	14.5	12	12.2	11.5	9
W occlusal	12	14.2	15	14	12	10.5
L ectostylid	0	present	present	–	present	0
W ectostylid	0					0
Protostylid	0	0	0	broken	0	0
Pli caballinid	+	+	0	–	+	0
AaO 2993	P2	P3	P4	M1	M2	M3
Wear stage	3	3	3	3	3	3
Height	16	17.5	–	–	–	[25]
L occlusal	31	24.5	25.1	23.5	23	28.5
Ante fossette	9	8.5	8	6	6.7	6.8
Double knot	15	16	16.6	14	15.6	13.5
Post fossette	12	12.5	13	9	10	10.7
W occlusal	14	15	17	13	14.5	14
L ectostylid	–	6	6	7	5	3.5
W ectostylid	–	4	4	4.9	4	3
Protostylid	isolated	pli	pli	pli	pli	+
Pli caballinid	0	0	0	0	0	0

CONCLUSIONS

— Although far from perfect, the use of *H. pomeli* as standard may be recommended for size comparisons of late African hipparions bones.

— There is no evidence of a marked sexual dimorphism in *H. pomeli.*

— The too frequent lack of association of bones, teeth, and skulls renders specific attribution of bones very awkward, but apart from the extremely large AL 155-1, the DD histogram is a good approximation of the size of *H. hasumense.* The latter was at least one standard deviation larger than *H. pomeli.*

Third metapodials. There are about 20 more or less complete adult MC IIIs and 35 MT IIIs, 15 of which are more or less entire (Table 14). In ratio diagrams, we use the minimal antero-posterior diameter of the medial condyle (no. 13 VE) rather than of the lateral condyle (no. 13 NY). The later was introduced only at the New York conference (Eisenmann *et al.* 1988) and most of our equid material was measured previously.

Table 9. Other permanent lower cheek teeth from Ahl al Oughlam.

	AAO 3554	AAO 4078	AAO 4072	AAO 4072	AAO 1435a	AAO 1435b	AAO 41
	P	P	P4	M1	M1	M2	M
Wear stage	3	3	2	2	2	2	1–2
Height	15	23	[26]	[27]	34	43	
L occlusal	27.5	26	25	24	25	25.6	24
Ante fossette	10	10.5	9	7	7.3	7.7	7
Double knot	17	17	16	15	15	14	15
Post fossette	13.3	14	13.5	8.7	10.9	11.2	10.3
W occlusal	16.5	16	16	13	15	14	14
L at 1 cm	27.2	26.5	25	24	23	23	
W at 1 cm	17.7	17	15	15.5	14.9	16.5	
L ectostylid	7	2	3.5	3.5 & 1		4	6 & 1
W Ectostylid	3.7	1	2.0	2.5		2.5	3
Protostylid	pli	pli	isolated	isolated	isolated	isolated	
Pli caballinid		0	0	0	0	0	0

	AAO 3550	AAO 1436	AAO 3135	AAO 1473	AAO 3541
	P2	P2	M3	M3	M3
Wear stage	4	3	2	2	3
Height	16	29	45	45	28
L occlusal	31	28.4	28	28.5	31.5
Ante fossette	7	8.4	8	8.8	8
Double knot	11.2	10	13	12.3	13
Post fossette	10.2	11.7	10.1	10	11
W occlusal	12.2	13.4	12	12.7	13
L at 2 cm			29.5	29	
W at 2 cm			12.4	12.5	
L at 1 cm			30	30	32
W at 1 cm			12.5	13	13
L ectostylid	1	0.5	2	1.5	2
W ectostylid	0.5	0.5	1	1	1
Protostylid	0	0	isolated		+
Pli caballinid	0	0		+	

Some scatter diagrams (not figured) show two sizes and/or morphologies: more or less robust, with more or less large proximal articular surfaces or distal widths. The coefficients of variation, however, are compatible with a monospecific sample. Table 15 gives the dimensions of some small and/or slender specimens of third metapodials not included in the statistical tables. They are probably subadult metapodials (like AaO-3707 and AaO-196) or juvenile.

Metacarpals. Compared with *H. mediterraneum* from the late Miocene of Pikermi (reference for the Simpson ratio diagram, Fig. 16), the AaO metacarpals are longer (no. 1), more robust (no. 3), wider at the level of the supra–articular tuberosities (no. 10), and have a more developed keel (no. 12).

Comparisons with other African hipparions are illustrated in Fig. 17. The closest resemblance is with the hipparion from Olduvai (mean of FLKN I 934, 7693, and SHK II 57/935), which is, however, more robust. From Koro Toro, Chad, one MC III (KT 96-17) is much more robust and has a more developed distal end; it falls outside the range of variation of AaO. The MC III from Ichkeul is longer than the average and seems more slender, but since it is not well preserved, most of its dimensions are uncertain. A metacarpal from Melka Kunturé, Gomboré II, seems close to those of Olduvai but is also poorly preserved. Most metacarpals from Hadar (not illustrated) are overall larger or have relatively larger distal ends (in particular the single specimen from the upper level AL 361-1, Kada Hadar member).

The development of the keel is an important character: functionally, it limits the lateral mobility of the articulation between third metapodials and first phalanges and facilitates sagittal 'pendular' movements. It is, however, difficult to quantify. To do so, Staesche & Sondaar (1979) have introduced the keel index: maximal antero-posterior diameter of the keel divided by the minimal antero-posterior diameter near the keel (percentage). Bernor *et al.* (2005) have greatly refined the estimation of keel development by also taking into account the size (scaling); in doing so, however, they were obliged to deal with relatively few specimens. We did no scaling – thus were able to use more specimens – and instead of calculating a percentage, we have considered the development of the keel as the difference between its maximal antero-posterior diameter and the minimal antero-posterior diameter of the medial condyle. When plotted versus the distal articular width of third metacarpals (Fig. 18), it appears – naturally enough – that the protrusion of the keel is related to the size of the MC III. A main group includes most of African hipparions: the relative development of the keel is roughly the same from Langebaanweg E and Olduvai (small form: l, m, n) to Olduvai (large form: o to u), including AaO, Hadar SH (d, i, j, k) and KH (b). Outside this main group, plot Omo F (5) and Roccaneyra (6) where the protrusion is maximal and more pronounced than in

Table 10. Permanent lower cheek teeth of Aïn Brimba. #: very small.

	1958.14.171 P4	1958.14.171 M1	1958.14.171 M2	1958.14.193 M2	1958.14.193 M3	1958.14.183 M2
Wear stage	0	1	0–1	1	0–1	2
Height			63		59	62
L occlusal	28	27	30	26.2	29	28
Ante fossette		10.1	11	8	8	8
Double knot		15.6	14	16	[12.5]	15.5
Post fossette		11.7	14	10.2	[9]	12
W occlusal	14	12	[11]	10.5	[8.5]	13
L at 2 cm	[28]					25
W at 2 cm						15
L at 1 cm						26
W at 1 cm						15
L first ectostylid		1		1	1, broken	1
W first ectostylid		1		1	1	1
protostylid		isolated	broken	isolated		0
Pli caballinid	1	0	1	0	1	#

	1937.11.21 P3	1958.14.175 P4	1958.14.179 M1	1958.14.184 M1	1957.11.10 M1	1958.14.183 section
Wear stage	2–3	2	2	2	2	3
Height	34	56	47	46	48	35
L occlusal	28.5	30	28	25.6	26	25.7
Ante fossette	10	14.2	7.8	8	7.7	7.8
Double knot	18.1	17	16	16	15.8	15.5
Post fossette	14.1	14.5	11	11	11.1	10.5
W occlusal	15	15	12	13.6	13	14.3
L at 2 cm	28	27	24.5	24		
W at 2 cm	16	16	14	14	15	
L at 1 cm	28	26	26	24.3	24.5	
W at 1 cm	16	16	14.3	15	15	
L first ectostylid	5.1	0.1		2	1	3.7
W first ectostylid	2.1	0.1		1	1	1
Protostylid		isolated	isolated	pli	pli	pli
Pli caballinid	1	1	1	0	0	0

	1957.11.20 P2	1958.14.229 P2	1958.14.177 P2	1958.14.178 M3	1958.14.176 M3	1958.14.174 M3
Wear stage	1–2	3–4	2–3	0–1	0–1	2
Height	44	25	37	57	60	48
L occlusal	[36]	34	34	[26]	28	30
Ante fossette	9	9	8	[8.7]	[13.5]	9
Double knot	12	14	13.1	[12.7]	[13]	14
Post fossette	15.5	15.5	15.8	[10]	[9]	11
W occlusal	13.5	13.5	14.7	[9.5]	[10.1]	11
L at 2 cm			33	30	30	30.3
W at 2 cm			13	13	13.3	12.2
L at 1 cm		33	32.8	30	30	31.1
W at 1 cm		15	13.2	13.2	12.5	13.2
L first ectostylid		2				1
W first ectostylid		1				1
Protostylid	0	0	0	not in wear	not in wear	isolated
Pli caballinid	#	0	1	1	1	0

dolichopodial hipparions (Venta del Moro, Maramena (1), Layna (2), Odessa (3), Sagajdak (4)). Minimal protrusion is found at Koro Toro, Chad (9) and in one specimen from Hadar DD2-3 (a). It is remarkable in that the keel seems relatively less developed in Hadar DD (c, e to h), and in particular less than in the contemporaneous Omo B (v, w). Mongolian (Shamar and Beregovaja) hipparions, whether more robust (*H. tchicoicum*) or more gracile (*H. houfenense*), plot with the main group. Not represented in Fig. 18, *Hipparion crassum* (Perpignan), *H. crusafonti* (Villaroya), and most of *H. heintzi* (Çalta), also plot with the main group.

Thus, it seems that the development of the keel cannot be directly related to geological age, nor to size, or gracility. Very probably, it is more related to environmental conditions that may select better adaptation to running in open landscapes, but local population idiosyncrasies cannot be excluded. It seems, therefore, risky to recognize lineages using keel development.

Metatarsals. Compared to *H. mediterraneum* (reference for the Simpson ratio diagram, Fig. 19), the AaO metatarsals are longer (no. 1), more robust (no. 3), proximally and

Table 11. Deciduous lower cheek teeth from Ahl al Oughlam. E1 and E2: first and second ectostylid. DK: Double knot.

	AaO 4070 dP2	AaO 4070 dP3	AaO 4070 dP4	AaO 2064 dP3	AaO 2064 dP4	AaO 3535 dP3
Wear stage	2	2	2	0–1	0–1	1–2
Height	–	–	–	28	34	17
L occlusal	31.5	29	31	31	34	31
Ante fossette	[9]	9	9			[8]
Double knot occlusal	12	15	15			15
Double knot maximal				[17]	[17]	
Post fossette	10.1	12.7	11.7			[11]
W occlusal	15	13	12.5			12.0
L ectostylid	1.5	3.5	2	present	present	present
W ectostylid	1	1.5	1.5			
Protostylid	0	pli	isolated	present	present	isolated
Pli caballinid	1	1	1			

	AaO 3136 dP2	AaO 3137 dP2	AaO 3169 dP2	AaO 3548 dP2	AaO 3597a dP2	AaO 4079 dP2	AaO 4080 dP2
Wear stage	1	0	0	0	0–1	0–1	0–1
Height	15	21	23	21	21	21	22
L occlusal	33	[33]	34	[34]	35.5	35	37
Ante Fossette	9						
Double knot occlusal	11	13	13	[13]	13	14	14
Double knot maximal		17	17	17.5	[17]	[19.5]	[19]
Post fossette	15						
W occlusal	11	11	11.5	10.5	11.3	13	12
Ectostylid	present		present	present	present	present	present

	AaO 2057 dP4	AaO 3138 dP3–4	AaO 3139 dP4	AaO 3140 dP3–4	AaO 3141 dP3–4	AaO 3142 dP3–4	AaO 3536 dP3–4
Wear stage	0–1	0–1	1	0–1	0–1	0	0–1
Height	[30]	27	25	26	24	26	22
L occlusal	35	[30]	32.5	31.5	31	31	31
Ante Fossette			8				
Double knot occlusal	14.5	13.5	14	14	14.5	15	15
Double knot maximal	[17]	[17]		[16]	[17.5]	[18]	
Post fossette			12				
W occlusal	10.5	10	11	10	11	11	11
top E1 from DK	11	10	3	12	8	11.5	
top E2 from DK		17	5.0			18.5	
L ectostylid maximal	6.5	6	[6.5]	9	7	6.5	
Protostylid	isolated	present	present	present	present	present	present

	AaO 3542 dP3–4	AaO 3544 dP3–4	AaO 3545 dP3–4	AaO 3547 dP3–4	AaO 3597b dP3	AaO 3597d dP4	AaO 4076 dP3–4
Wear stage	1	0–1	1	1	0–1	0–1	0–1
Height	26	26	21	23	21.5	23	27
L occlusal	[32]	32		30	[30]	[32]	31
Ante fossette			8	9			
Double knot occlusal		13	14	13.5	15	14.5	10.5
Double knot maximal	[17.5]	17	[19]	[16.5]	[17]	[18]	[16]
Post fossette			13	13			
W occlusal	11	9	11	10	11	10	9.5
top E1 from DK	11	8	5	2	10	[10]	6.5
top E2 from DK		14			17	[20]	11.5
L ectostylid maximal	8	6	[6]		7	7	6
Protostylid	present	present	present	present		present	present

distally deeper (nos. 6 & 12), and have much more developed distal widths (nos. 10 & 11). The single and incomplete MT III of Kvabebi (Vekua 1972; Alberdi & Gabunia 1985) is smaller but otherwise similar to the average of AaO; so are, to a lesser extent, the MT IIIs of Villaroya and Roccaneyra. No African Plio-Pleistocene metatarsals resemble those of AaO, the less dissimilar being those from Olduvai and Koro Toro, Chad (Fig. 20).

The scatter diagram of keel development (not figured here) carries less information than for the third metacarpals. However, another feature seems interesting because it expresses approximately the position of the lateral digits: when they are placed more ventrally, the diaphysis is narrower and deeper (Fig. 21). The deepest diaphyses are

Table 12. Statistics of Höwenegg limb bones widths from Bernor *et al.* (1997) and of *H. pomeli*. $\bar{x}$: mean, *s*: standard deviation, *n*: number of specimens, min: minimal observed value, max: maximal observed value. Tibia diaphysis, supposed: values used in this paper (see text).

Bernor *et al.* 1997	$\bar{x}$	s.e.	*n*	min	max
Humerus distal articular	70.46	2.66	13	65.3	74.1
Radius proximal maximal	69.23	1.77	13	65.8	72
Radius distal maximal	64.13	2.04	12	61.5	67.8
MC III proximal articular	39.92	1.05	16	37.7	41.9
MC III distal articular	37.09	1.6	12	33.7	39.9
PH I anterior diaphysis	29.1	1.47	12	27.1	31.2
PH II anterior diaphysis	31.85	1.17	15	30	34.5
PH III anterior articular	41.05	2.52	8	38	45
Tibia diaphysis	[42.6]	[5.61]	13	[32.4]	49.2
Tibia diaphysis	44.6	2.00	13		49.2
Tibia distal maximal	70.14	1.86	19	66.7	73.4
Talus distal articular	44.78	1.81	21	40.5	48.1
MT III proximal articular	41.77	2.09	18	37.3	46.5
MT III distal articular	37.77	1.89	23	34.9	42
PH I posterior diaphysis	30.87	1.47	12	28.1	33
PH II posterior diaphysis	31.34	1.07	11	29.2	33
PH III posterior articular	36.43	1.34	4	35	38.2

H. pomeli	$\bar{x}$	s.e.	*n*	min	max
Humerus distal articular	73.4	2.69	6	69	76.5
Radius proximal maximal	73	2.83	11	67	78.2
MC III proximal articular	46.3	2.01	20	42.5	49.6
MC III distal articular	42.0	1.19	26	39.6	44.2
PH I diaphysis	33.3	2.13	7	30	37
PH II diaphysis	37	1.75	9	35.3	40
PH III articular	42.7	2.99	13	37	48
Tibia diaphysis	47.4	2.99	10	46	53
Tibia distal maximal	70.9	2.03	8	68	73
Talus distal articular	48.5	2.35	33	43.5	54
MT III proximal articular	45.3	1.66	35	42.3	49
MT III distal articular	43.2	1.18	25	40.7	45

found in dolichopodial hipparions (Venta del Moro, Maramena (1), La Gloria (2)) but also in some specimens from Langebaanweg E and Olduvai. The widest and flattest diaphyses occur at Çalta (*H. heintzi*), Omo C (10), Hadar, and in *H. turkanense* (11). In Vallesian species, the diaphysis may be very wide and flat (Eppelsheim, 12), or much less (Esme Akçaköy). Not illustrated *H.* cf. *houfenense* of Shamar and Beregovaja and *H.* cf. *crusafonti* of Kvabebi plot with the intermediate group together with AaO.

Phalanges of the third digit: first phalanges. In most species of *Equus,* it is possible to discriminate anterior and posterior phalanges (Dive & Eisenmann 1991). This discrimination is more difficult in hipparion. Nevertheless, a scatter diagram of the proximal depth versus the distal articular width (Fig. 22) gives good results: in samples of first phalanges associated with third metapodials (Höwenegg, Hadar, Shamar, Layna, Grebeniki) or determined by Gromova (1952) (*H. elegans* from Pavlodar, *H. moldavicum*) and Gabunia (1959) (Khadjibi, Chobruchi, Kuialnik), the proximal depth is relatively larger when the phalanx is posterior. Moreover, within the same species, anterior first phalanges are usually more slender. According to these criteria, we have at AaO four anterior, and three posterior, phalanges (Table 16). The best preserved anterior phalanx (AaO 1261, Fig. 23B) is small and may belong to a not fully grown individual. On the ratio diagram (Fig. 24) it compares well with a specimen from Olduvai M-14456c (possibly Bed I), which is, however, more slender. Similar proportions are found in the much larger AL 161-1 (Hadar DD) and in the much smaller Omo 1974-263-573 (member C ?). The other anterior phalanges of AaO are larger and more robust.

One of the posterior PH Is associated with a MT III and a second phalanx (AaO-196) is badly preserved and looks very small. It could fit with the anterior AaO-1261.

On the ratio diagram (Fig. 25), AaO-2838 resembles two Tanzanian phalanges (Olduvai SHKII 1957.1165 and Laetoli M 31934) and also AL 194-2 of Hadar (DD). Specimen AaO-2844 (Fig. 23A) is more like AL 155-6 (Hadar DD).

Second phalanges. Second phalanges may be sorted into anterior or posterior by plotting the distal articular breadth versus the maximal length: posterior phalanges are relatively narrower. They are also deeper at the proximal end. According to these characters, there are four anterior and five posterior phalanges at AaO. The sample appears monospecific (Table 17).

Third phalanges. It is simple to distinguish anterior from posterior third phalanges of the same individual, for example in Hadar AL 155-6 (Table 18), the anterior being wider at the sole and having wider and more shallow articular surfaces. But the intraspecific variation is very large and assignment of a particular specimen is often uncertain in unassociated bones. At AaO (Fig. 23C,D), three third phalanges are certainly anterior and two are certainly posterior. The assignment of the rest is tentative.

Other limb bones. Compared to the extant *Equus grevyi* and the fossil *Allohippus vireti* the variation of the talus is large (Table 13; Fig. 23E), but all attempts to split the sample were unsuccessful. Measurements of other limb bones are in Table 19.

Limb bone segments. In *Equus* and *Hipparion,* the relative lengths of limb bones give useful information about cursorial abilities; information on the ground (hard or heavy) is provided by the relative width of the third phalanges (Eisenmann 1984, 1991; Eisenmann & Sondaar 1998). Schematically, third phalanges are narrow when the ground is hard; proximal limb bones are relatively short when species are cursorial. Until now there were no good data on monospecific whole (associated) skeletons of hipparions, so that in the past (Eisenmann & Sondaar 1998), ratio diagram comparisons were made with the extant *E. hemionus onager.* But now we are able to use as reference the Höwenegg sample (Bernor *et al.* 1997, and V.E. unpubl. data; Table 20). For humeri and femora, we use articular lengths; for the third phalanx, we use the solar width of the anterior phalanx; for all other bones, we use maximal lengths.

There is only one associated skeleton of African hipparion (AL 155-6 of the Denen Dora member of Hadar), presumably belonging to *H. hasumense,* and few samples rich enough for using reliable average dimensions. A ratio diagram (not illustrated) has shown no great differences between the proportions of the possible juveniles and the other bones of AaO, justifying the use of

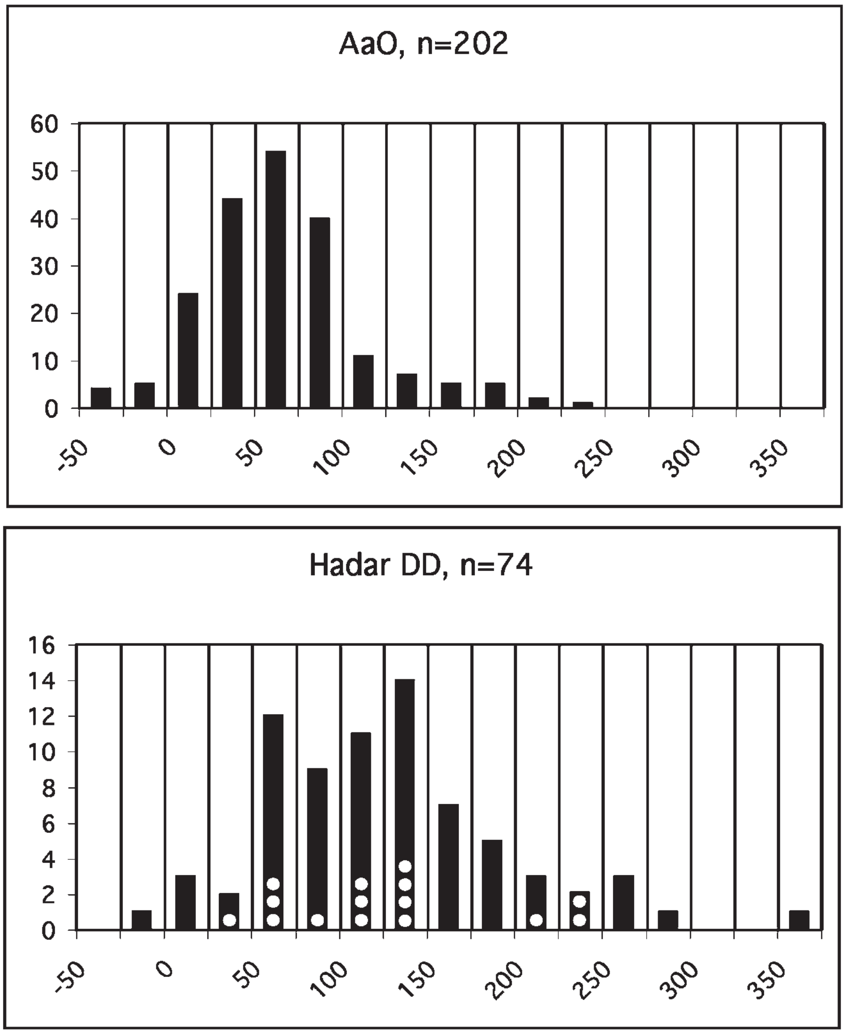

Figure 12. Variation Size Indices for AaO and Hadar DD hipparion samples, using Höwenegg as standard. *n*: number of widths. White points for AL 155-6-associated limb bones.

Table 13. Statistics for tali of the AaO sample, for the extant *E. grevyi,* and for the fossil *Allohippus vireti*. Abbreviations as for Table 12, plus c.v.: coefficient of variation (c.v. = 100 × s.e./$\bar{x}$). 1: maximal length, 2: maximal diameter of the medial condyle, 3: maximal breadth, 4. breadth of the trochlea at the apex of each condyle, 5: distal articular breadth, distal articular depth, 7: maximal medial depth.

AaO	*n*	$\bar{x}$	min	max	s.e.	c.v.
Greatest length	40	63.3	58.5	69.0	2.86	4.52
Medial length of trochlea	38	61.1	54.5	67.5	2.58	4.22
Maximal width	36	59.8	53.0	68.0	3.02	5.05
Trochlear width	40	29.6	26.6	32.0	1.43	4.83
Distal articular width	33	48.5	43.5	54.0	2.35	4.85
Distal articular depth	37	35.0	31.5	38.4	1.54	4.40
Medial depth	33	50.2	44.5	58.0	2.50	4.98
E. grevyi						
Greatest length	28	64.7	60.5	68.0	1.87	2.89
Medial length of trochlea	28	62.7	60.0	65.6	1.36	2.17
Maximal width	28	61.8	56.0	66.0	2.20	3.57
Trochlear width	28	28.9	26.0	31.0	1.59	5.52
Distal articular width	28	51.0	47.0	55.5	1.94	3.81
Distal articular depth	28	35.8	33.0	39.0	1.64	4.57
Medial depth	28	52.6	49.5	55.5	1.76	3.34
Allohippus vireti						
Greatest length	105	66.5	60	73	2.52	3.79
Medial length of trochlea	109	65.5	60	70	2.35	3.58
Maximal width	110	66.9	60	72.5	2.63	3.93
Trochlear width	114	31	27.5	34.5	1.36	4.39
Distal articular width	102	54.9	51	59.5	1.77	3.21
Distal articular depth	108	37.5	35	41	1.42	3.79
Medial depth	100	55.3	49.5	59.5	1.85	3.35

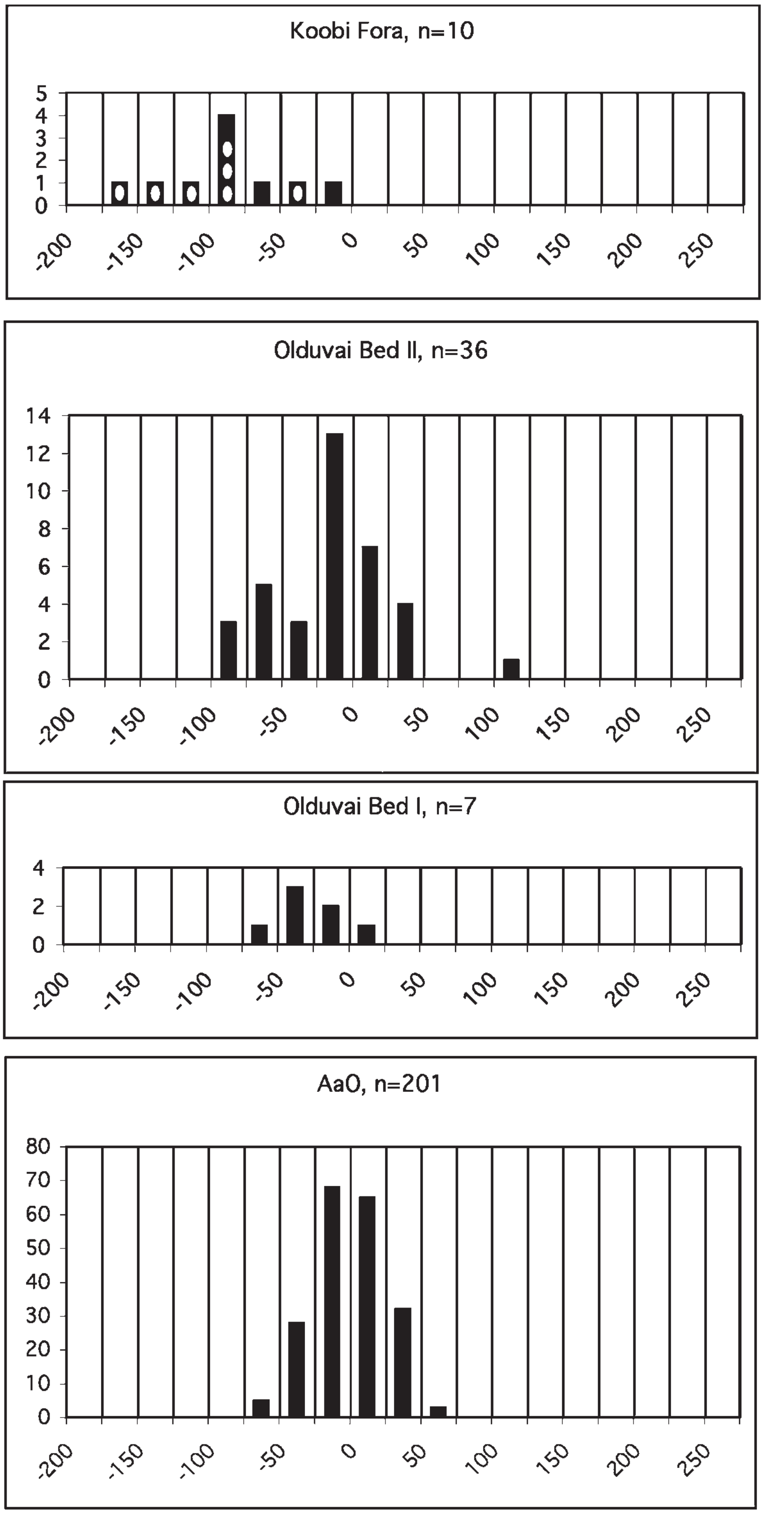

Figure 13. Variation Size Indices using AaO as standard for Olduvai Bed I, Bed II, and Koobi Fora. White ellipses for KBS member specimens.

average dimensions. Figure 26 compares *H. hasumense* AL 155-6, *Hipparion heintzi* of Çalta, the sample of Langebaanweg E, and *H. pomeli.* The very short metapodials of *H. heintzi* are a good indication of poor cursorial adaptation. By contrast, *H. hasumense* and *H. pomeli* were probably better runners. Moreover, at Höwenegg and Çalta, the femora and radii are of subequal length, while in *H. pomeli* (like in all extant *Equus*) the radius is much longer. The proportions of the Langebaanweg *E. hipparion* are similar to those of *H. pomeli.*

The cursorial adaptations of *H. pomeli* from Ahl al Oughlam agree well with the environment of the locality, where the abundance of alcelaphines and antilopines among bovids suggest an open landscape.

ADDITIONAL NOTES: *H. HENDEYI* SP. NOV. FROM LANGEBAANWEG E AND *H.* AFF. *CRASSUM* FROM KOSSOM BOUGOUDI, CHAD

Langebaanweg E

Hooijer (1976) referred to *H.* cf. *baardi* the material from

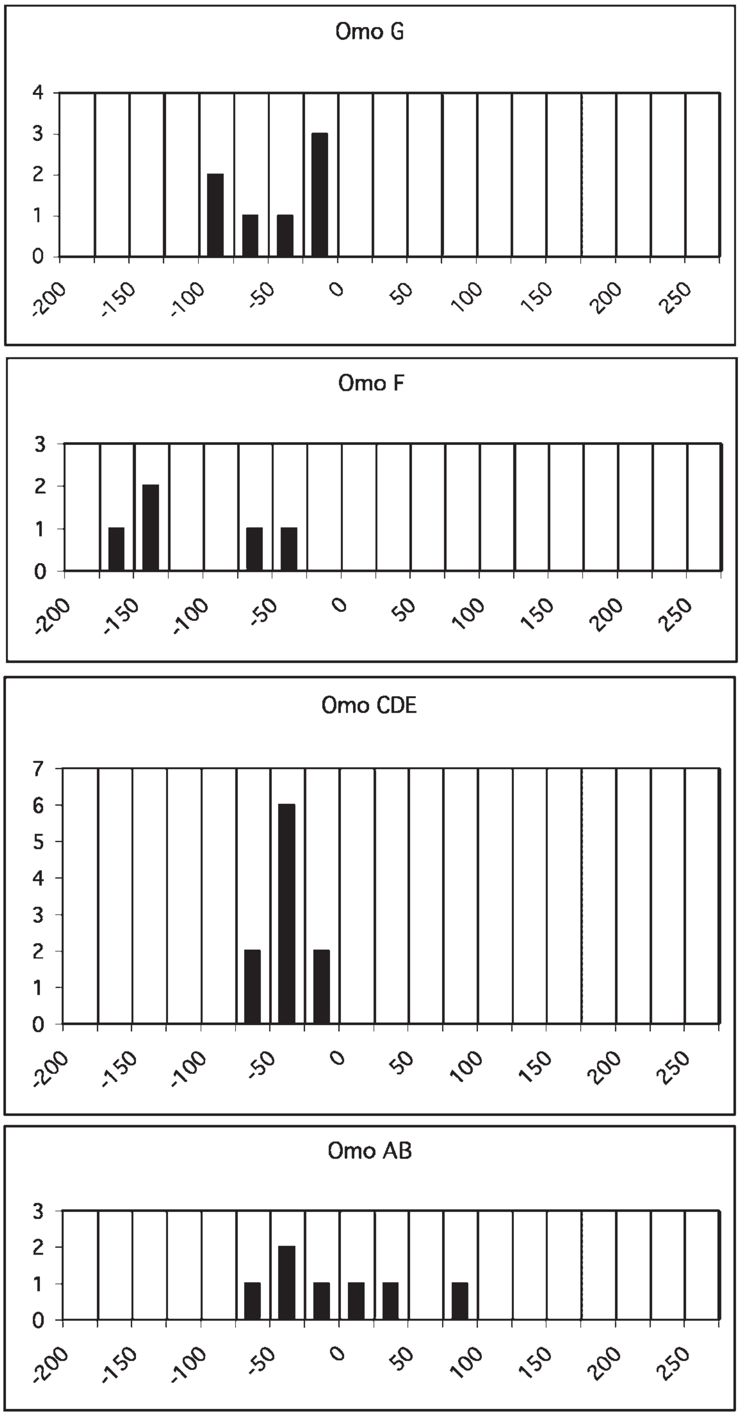

Figure 14. Variation Size Indices using AaO as standard for Shungura Formation (Omo).

Langebaanweg E Quarry, South Africa. Hendey (1978) correctly pointed that the hipparion of Quarry E was very different from *H. baardi* of Baard's Quarry and gave measurements of the lower cheek teeth. We propose to name this hipparion *H. hendeyi,* and choose as holotype the complete skull of an old female, L 22187, from Langebaanweg E, preserved in the Iziko South African Museum, Cape Town, and figured by Hooijer (1976, plate 1). The skull (Table 1) has a very long vomer–palate distance, a very faint POF, and a long and narrow muzzle; the cheek teeth of the skull are too worn to provide information on their dimensions but according to Hendey's data the lower series was about 152 mm long. On the whole, the skull resembles *H. giganteum* and *H. verae* of Grebeniki (Appendix Fig. 5), *H. moldavicum* of Taraklia, and possibly *H. feibeli* from Ekora-Kanapoi (Fig. 27). The cheek teeth of Quarry E are hipparionine, although some are hypsodont; the lower incisors are grooved (Hooijer 1976, plate 2-6; plate 8, fig. 2). The MC IIIs have well-developed keels (Fig. 18) exceptional in a species which is not dolichopodial. Two MT IIIs (L 5899 and L 21827) have very wide diaphyses and do not fit with the rest of the sample (Fig. 21).

Chad, Kossom Bougoudi 9

A fragment of skull, KB 9-97-13, dated to about 5 Ma. (Brunet *et al.* 2000), is remarkable in its very large dimensions (Table 1). The POF is situated at about 40 mm in front

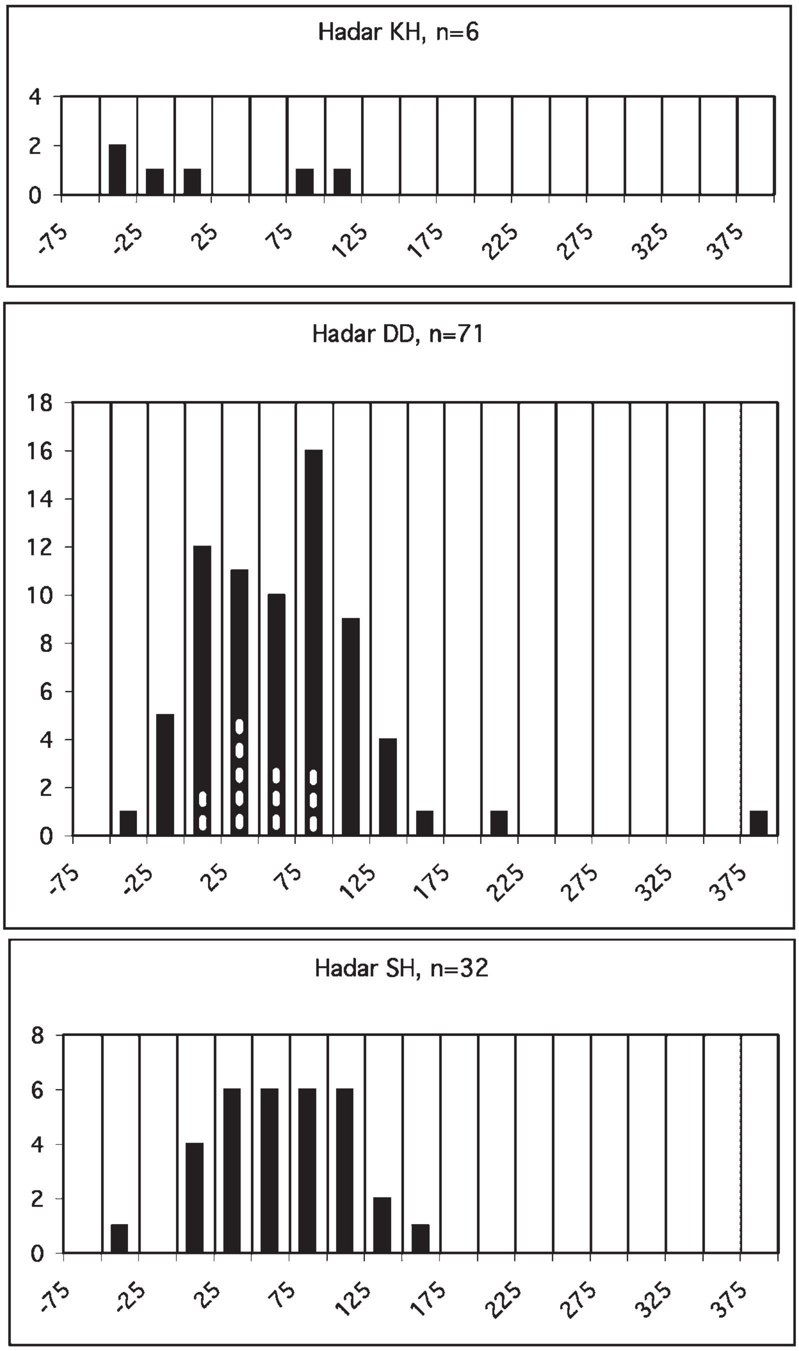

Figure 15. Variation Size Indices using AaO as standard for Hadar Formation. White ellipses for AL 155-6-associated bones.

of the orbit. The fossa is very well delimited at its anterior and dorsal borders, but not well delimited ventrally and posteriorly. The vomer–palate distance is long. The premolars and M1 are much worn; the less worn M2 and M3 are plicated.

This skull differs from *H. proboscideum* of Samos by the presence of only one POF instead of two (Koufos & Vlachou 2005), the long vomer–palate and P2–orbit distances. On the whole, it resembles best *H. dermatorhinum* from China (data Bernor *et al.* 1990; V.E., unpubl. data) and possibly *H. crassum* and *H. tchicoicum*, judging by the dimensions of the mandibles Pp 208 from Perpignan and Shamar 3381-53 (Table 2). *H. garedzicum magianense* of Sor, Tadjikistan (Zhegallo 1978) very probably belongs to the same group (Table 1; Fig. 28).

DISCUSSION

Like some other authors (Koufos & Vlachou 2005), we use *Hipparion* as a generic name for all Old World late Miocene equids without distinguishing the numerous complexes to which they may belong. We prefer also not to give specific names to isolated limb bones or teeth.

Bernor & Armour-Chelu (1999a) have presented a comprehensive overview of hipparions in general and more particularly of African forms. According to them, there were only two founding populations in Africa. The first derived from the *Hippotherium* complex, which includes (among other species) the European *H. primigenium* and *H. giganteum*, the Chinese *H. dermatorhinum*, and the African *H. africanum*. The second founding population derives from the *Sivalhippus* complex, which includes among other species, the Siwaliks *S. perimense* and the

Table 14. Statistics for third metacarpals and metatarsals from Ahl al Oughlam. Abbreviations as in Table 13.

	MC	*n*	$\bar{x}$	min	max	s.e.	c.v.
Maximal length	1	19	237.6	226	254	7.23	3.04
Minimal breadth	3	25	32.7	30.8	35	1.11	3.40
Depth at level of 3	4	22	27.6	26	30.4	1.09	3.96
Proximal articular breadth	5	20	46.3	42.5	49.6	2.01	4.33
Proximal depth	6	20	31.8	29	34.4	1.54	4.84
Distal max. supra–articular breadth	10	28	44.6	42.1	47.1	1.36	3.05
Distal max. articular breadth	11	26	42	39.6	44.2	1.20	2.85
Distal max. depth of keel	12	25	35.2	33.2	37	0.99	2.80
Distal min. depth of medial condyle	13 VE	28	28.7	27.7	30.2	0.70	2.45
Distal min. depth of lateral condyle	13 NY	5	28.7	27.7	29.5	0.73	2.55
Distal max. depth of medial condyle	14	25	30.8	29.3	33	0.84	2.74
Max. diameter of 3rd carpal facet	7	22	39.6	35.6	41.5	1.70	4.29
Max. diameter of 4th carpal facet	8	21	11.9	10	14	1.02	8.52
	MT	***n***	$\bar{x}$	**min**	**max**	**s.e.**	**c.v.**
Maximal length	1	15	282.3	277.0	288.0	3.28	1.16
Minimal breadth	3	18	32.1	30.5	34.3	0.93	2.91
Depth at level of 3	4	21	32.44	30.3	34.0	1.05	3.25
Proximal articular breadth	5	35	45.3	42.3	49.0	1.66	3.66
Proximal depth	6	30	39.0	35.5	43.2	1.49	3.81
Distal max. supra–articular breadth	10	25	47.1	44.7	50.5	1.78	3.78
Distal max. articular breadth	11	25	43.2	40.7	45.0	1.18	2.72
Distal max. depth of keel	12	26	36.9	35.1	38.7	1.03	2.8
Distal min. depth of medial condyle	13 VE	27	29.0	27.8	30.0	0.65	2.25
Distal min. depth of lateral condyle	13 NY	6	28.2	27.2	29.0	0.59	2.08
Distal max. depth of medial condyle	14	24	31.9	29.7	33.6	0.91	2.85
Max. diameter of 3rd tarsal facet	7	32	41.8	38.0	44.5	1.56	3.73
Diameter of 4th tarsal facet	8	24	10.0	8.5	11.3	0.76	7.58

Chinese *Plesiohipparion houfenense*, as well as the European *Pl. crassum* (Bernor & Armour-Chelu 1999b). Bernor & Armour-Chelu consider *S. perimense* as the sister group of *Eurygnathohippus* within which are placed *H. turkanense* and all the post-Miocene African hipparions.

In 2003, Bernor & Harris wrote that the POF of *Eurygnathohippus* aff. *feibeli* of Ekora 'suggests relationships within the *Cormohipparion-Hipparion-Hippotherium* trichotomy while *Eurygnathohippus turkanense*'s reduced POF and limb proportions suggest an alliance between *E. turkanense* and *S. perimense*. The occurrence of ectostylids in Lothagam *E. turkanense* and *E. feibeli* suggests a phylogenetic relationship exclusive of Eurasian hipparions and inclusive with Plio-Pleistocene African hipparions'.

Still more recently, Zouhri & Bensalmia (2005) made a thorough revision of Old World hipparions. They recognize four genera: *Hippotherium*, *Cremohipparion (*including *Cr. moldavicum* as a synonym of *Cr. mediterraneum), Hipparion*, and *Proboscidipparion.* The latter is subdivised into three subgenera: *Proboscidipparion, Plesiohipparion,* and *Eurygnathohippus*. They rightly point that *H. crassum* cannot be considered as a *Plesiohipparion* because of the primitive pattern of its lower cheek teeth, and rightly exclude *H. turkanense* from *Eurygnathohippus* because it has neither the typical lower cheek teeth nor the reduction of the third incisors of *Eurygnathohippus.*

1. Discussion of Bernor & Armour-Chelu (1999a) and Bernor & Harris' (2003) opinions

Our first point of disagreement concerns the definition

Table 15. Metapodials from Ahl al Oughlam. Measurements as in Table 14.

	MC AaO 194	MC AaO 2831	MC AaO 3706	MC AaO 3707	MC AaO 3725
1	230			240	
3	28.2	28.6	28.7	28.8	
4		24.3	22.4	25.5	
5	44.8		43	45.5	
6				31.8	
10				41.2	40.8
11					39.2
12				33.7	34.4
13 VE				27	27.3
13 NY				25.8	27.2
14				28	29.6
7	38		35.5	39.2	
8	10		11	10.4	

	MT AaO 196	MT AaO 4440	MT AaO 1514	MT AaO 3725b
1	275			
3		29.5		
4	34.2	33.8		
5		45.7		
6		36.5		
10	42.5		44	40.8
11	41		41	40.4
12	33.7		35.1	34.5
13 VE	28.4		27.8	27.9
14	31.5		30.3	29.6
7		42.5		
8		13.3		

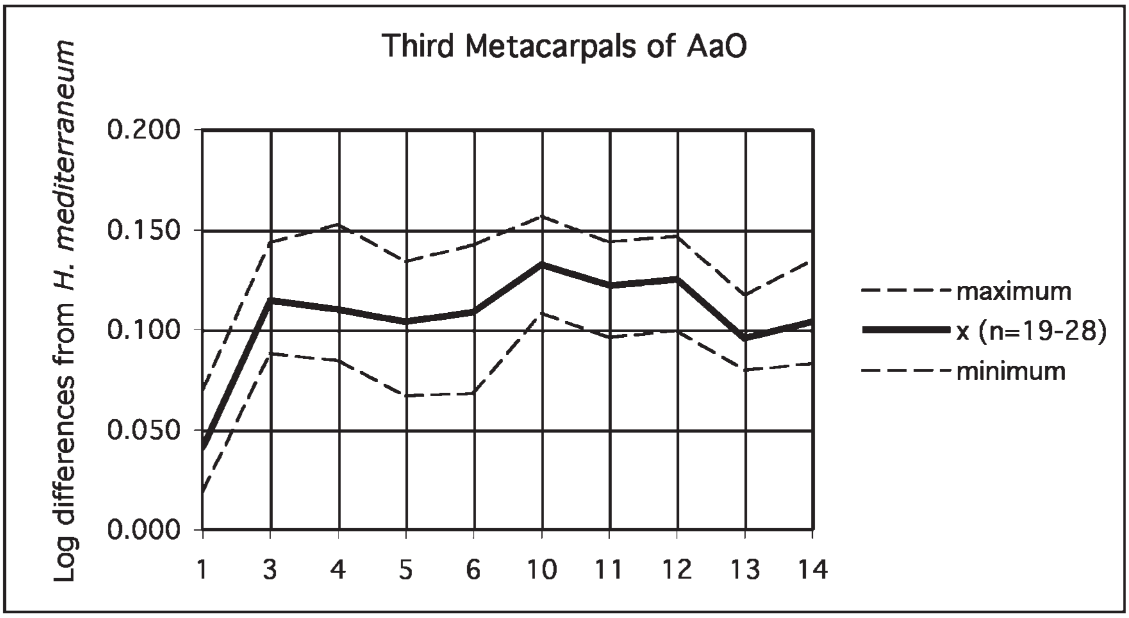

Figure 16. Ratio diagram for AaO third metacarpals maximal, average ($\bar{x}$), and minimal values. Measurements as in Table 14.

of *Eurygnathohippus.* All late hipparions – not only African – exhibit many apomorphies. But synapomorphies are not so evident.

a) The grooved lower incisors are not a synapomorphy of all African late hipparions since they are present in *H. moldavicum* (Chobruchi), *H. giganteum* (Grebeniki), *H. crassum* (Perpignan), and *H. houfenense.* On the other hand, the incisors of AL 155-6 (Denen Dora of Hadar) are not grooved, while they are grooved in AL 177-21 of the same member, and in AL 59-9B of the earlier Sidi Hakoma member. Both grooved and not grooved incisors are represented in Omo member C.

b) The cheek teeth of late hipparions present many apomorphies. Most are probable homoplasies related to grazing hard food. Such are the hypsodonty, the elongated and narrow protocones, the angular double knots, the development of protostylids, the straightening of the vestibular enamel ridges, and the development of vestibular enamel structures between protoconid and hypoconid. As already pointed out (and partly illustrated) by Forstén (1997a,b), the latter are similar in general, but different in detail. In *H. huangheense* from China (FAM 11820), a posterior pointed extension of the protoconid may be a functional equivalent of the pli caballinid/ectostylid complex. In *H. crusafonti* from Villaroya, the pointed extension of the protoconid is present but less marked than in *H. huangheense.* In *H.* cf. *crusafonti* of Kvabebi there are very well-developed plis caballinids (but no extension of the protoconid); moreover, there are well developed plis protostylids on dp2 (Fig. 29).

The only cheek tooth synapomorphy of late hipparion

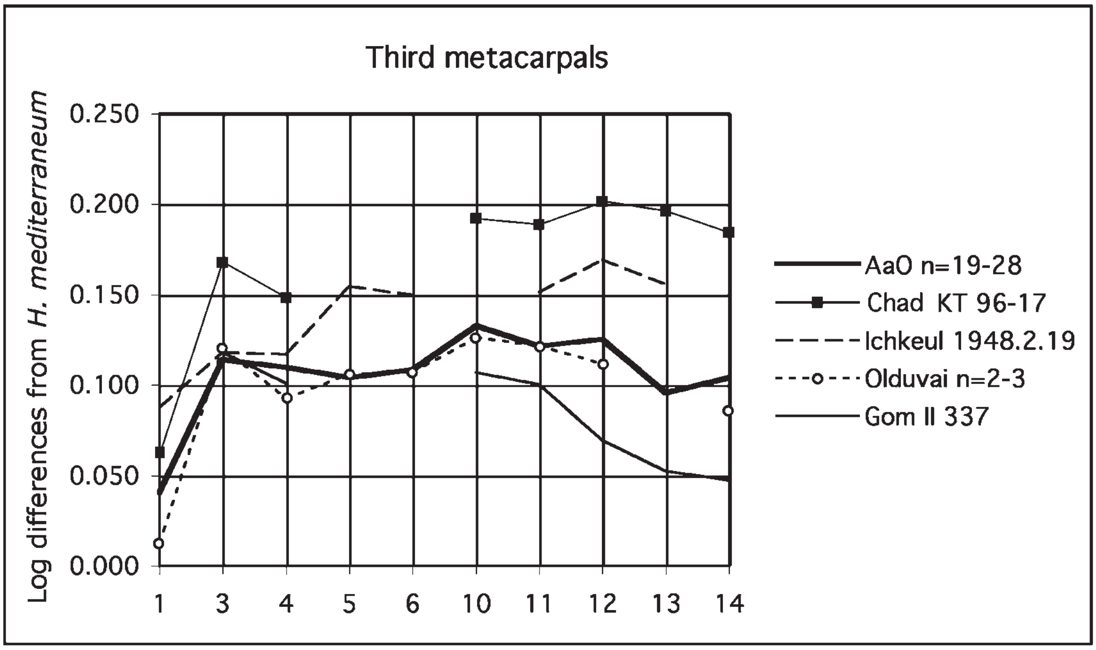

Figure 17. Ratio diagram comparing average AaO third metacarpal to metacarpals of Chad, Ichkeul, Olduvai (FLKNI 934 and 7693, SHKII 57/935), and Melka Kunturé. Measurements as in Table 14.

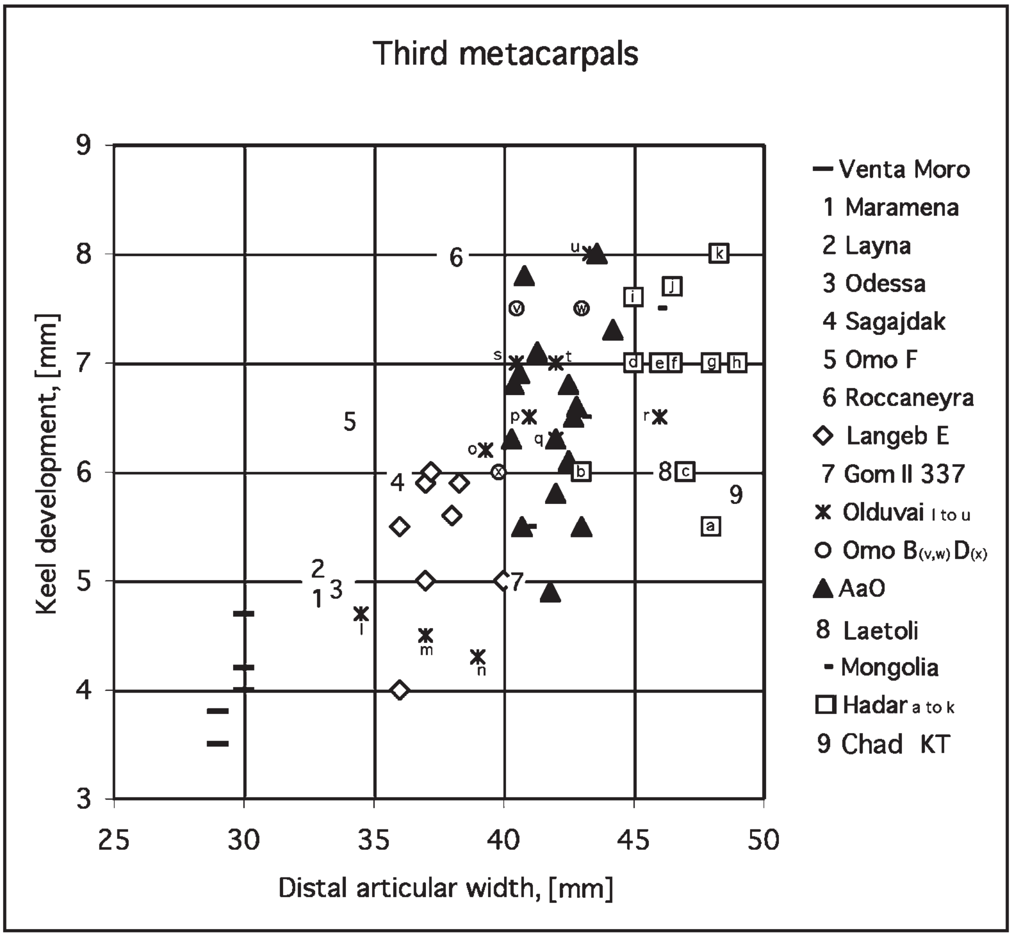

Figure 18. Scatter diagram (mm) of third metacarpal keel development versus distal articular width. Hadar: a: 116-33, DD2-3; b: 361-1, KH; c: 99-38, unknown; d: 327-14A, SH2; e: 115-6BB, DD2; f: 150–1, DD; g: 212-3, DD2-3; h: 315-9C, DD2-3; i: B 236-7, SH2-3; j: B 147-20, SH2-3; k: 107-15, SH2-3. Olduvai: l: 1963/2750, subadult, BK II; m: M 16985, unknown; n: 57/576, subadult ?, SHK II; o: 59/366, LGK; p: F 345, unknown; q: 7963, FLKN I; r: F 811, S4 1941; s: 933, FLKN I; t: 57/935, SHK II; u: 1952/307, BK II. Omo B: v: 3004-41; w: 3005-41. Omo D: x: 73-2626.

from African would be the development of ectostylids as functional equivalents of plis caballinid or protoconid extensions. But ectostylids are clearly visible on the occlusal surfaces of the molars of BMNH 26211 from Bhandar Bone Bed of Dhok Pathan (Forstén 1997b, fig. 16A). On the other hand, they are not developed in the Laetoli specimens, and in those from Baard's Quarry at Langebaanweg, and they are not expressed in *H.*

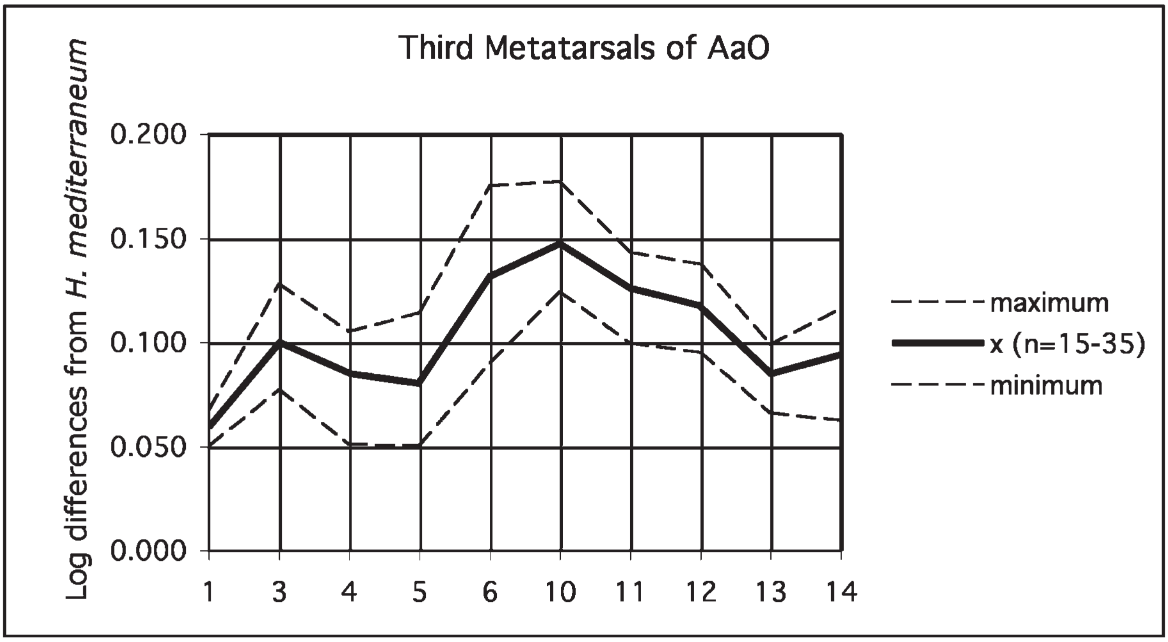

Figure 19. Ratio diagram for AaO third metatarsals maximum, average ($\bar{x}$), and minimum values. Measurements as in Table 14.

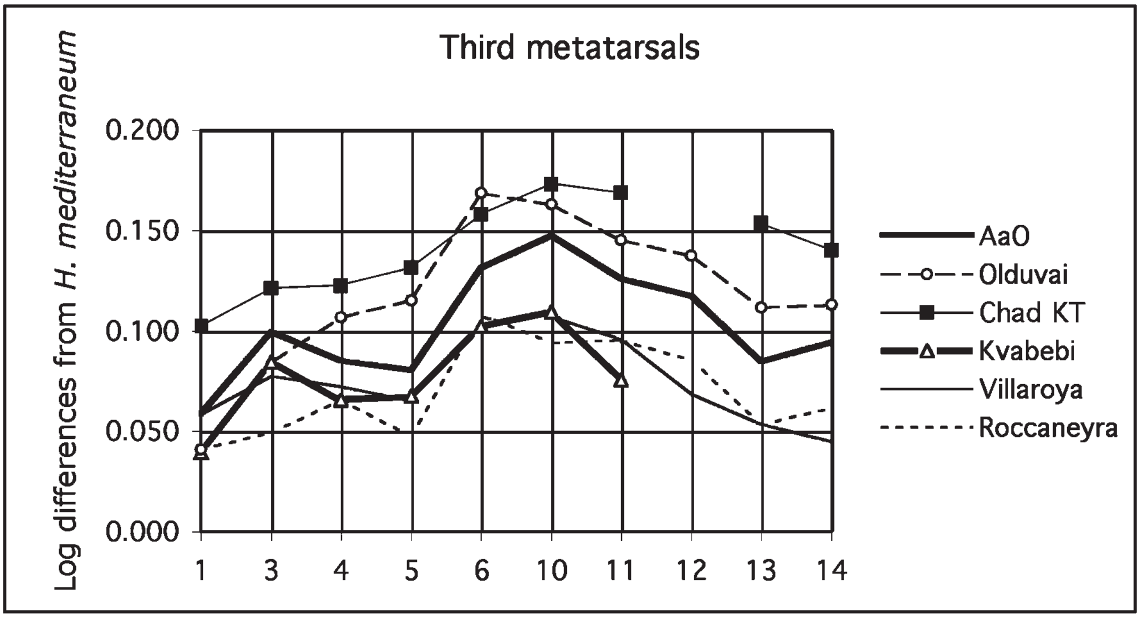

Figure 20. Ratio diagram comparing average AaO third metatarsal to metatarsals of Olduvai (BKII 1953-435, 1953-135, 1963-620; unknown 807 and 1-6), Chad KT13 (96-21, 39, 489), Roccaneyra (1948-13-11), Villaroya, and Kvabebi (KV 1082). Measurements as in Table 14.

turkanense from Lothagam Lower Nawata, appearing only in the Upper Nawata member.

c) In our opinion, the main point is the structure of the vomer and the basi-cranial 'caballine' proportions (vomer distances from the palate and the basion). They constitute solid synapomorphies for *H. afarense* and the *H. cornelianum* of East Turkana. The Chinese *H. houfenense s.s.* (type skull THP 10508) possibly had the same kind of vomer, because of its apparently long basion–vomer distance (Qiu, pers. comm.) but we are not certain of that since the skull is badly preserved. In *H. huangheense* (FAM 11820) the structure of the vomer and the

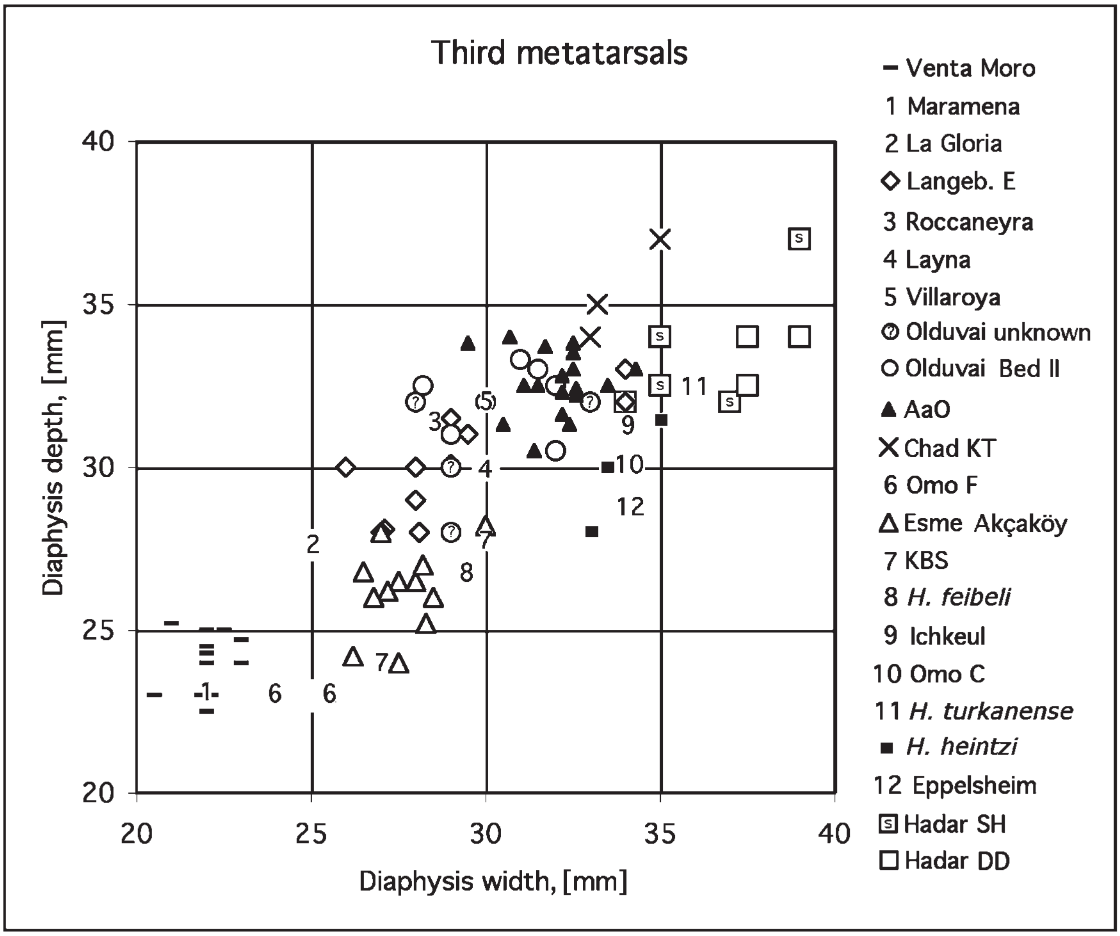

Figure 21. Scatter diagram (mm) of third metatarsal diaphysis depth versus diaphysis width.

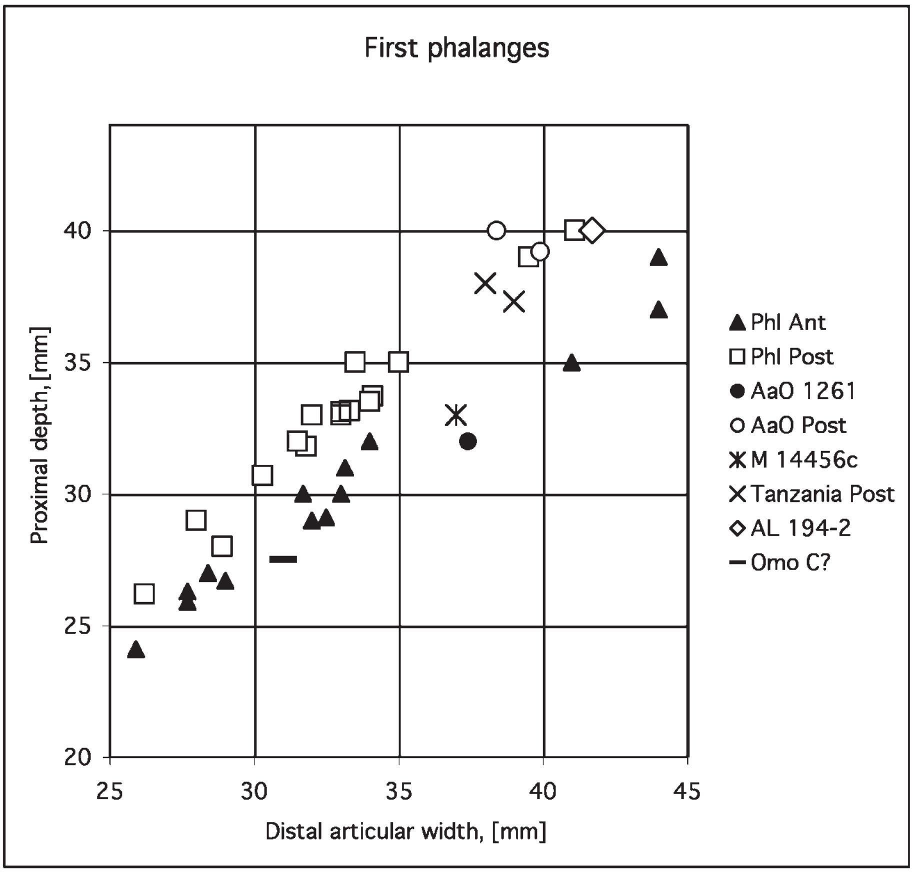

Figure 22. Scatter diagram (mm) of first phalanges of the third digit proximal depth versus distal articular width. Ant: anterior phalanges, Post: posterior phalanges. Data in Table 16.

basi-cranial proportions are uncertain owing to incomplete preparation. In *H. crusafonti* of Villaroya, the basi-cranial proportions are not known. In *H.* cf. *crusafonti* of Kvabebi, the distance from vomer to palate seems short but the morphology of the vomer and the distance between vomer and basion are unknown. When we studied the skull of *Sivalhippus perimense*, the basicranium was not fully prepared, so that information on this important point is again lacking. It is quite clear, however, that *H. turkanense* did not possess any of the basi-cranial characters shared by *H. afarense* and *H. cornelianum.*

d) Short, squarish, and broad arcades, without the reduction of I3, are not uncommon in hipparions. The best example is the well-known Greek *H. dietrichi*, but similar

Table 16. First phalanges of the third digit (PH I). W: width.

PH I		Ahl al Oughlam			Hadar DD		Omo C?	Olduvai Bed I?	Chad KT	Pikermi
	Anterior	AaO 1261	AaO 2839	AaO 3845	AL 155-6X	AL 161-1	1974.263 573	M 14456c A	13.96.42	M 47800
Maximal length	1	65.8	68.5	67.1	75	80	64	71.5	85	61.8
Minimal width	3	30	33.5	32.2	37.9	33	25	30.5	40.5	32
Maximal prox. W	4	42.8	47.7	45	52	49	36	44	57.5	45.5
Maximal prox. depth	5	32	36.4		39	37	27.5	33	43	33
Dist. supra–artic. W	7	37.4	38.8	40	44	44	31	37	48	34.7
Dist. articular width	6	36.3	39.4	38.6	45.5	44	30.5	37	48.5	35
Dist. articular depth	8				26.1				31	22.1

		Ahl al Oughlam			Hadar DD			Olduvai	Laetoli SHKII
	Posterior	AaO 2838	AaO 2844	AaO 196	AL 155-6AA	AL 161-2	AL 194-2	1957.1165	M 31934 P
Maximal length	1	67.5	70.5	62.4	70	76	72	69	67
Minimal width	3	34.2	37	32.6	38	34	36	34.2	33
Maximal proximal W	4	46.5	51.5	[43]	52	46.5	48	47.2	45
Maximal prox. depth	5	40	39.2	[32]	40	39	40	37.3	38
Dist. supra–artic. W	7	38.4	39.9	[39]	41.1	39.5	41.7	39	38
Distal articular width	6	38.8	39.9	38	43	40	41.2	39	36
Distal articular depth	8				26		28		

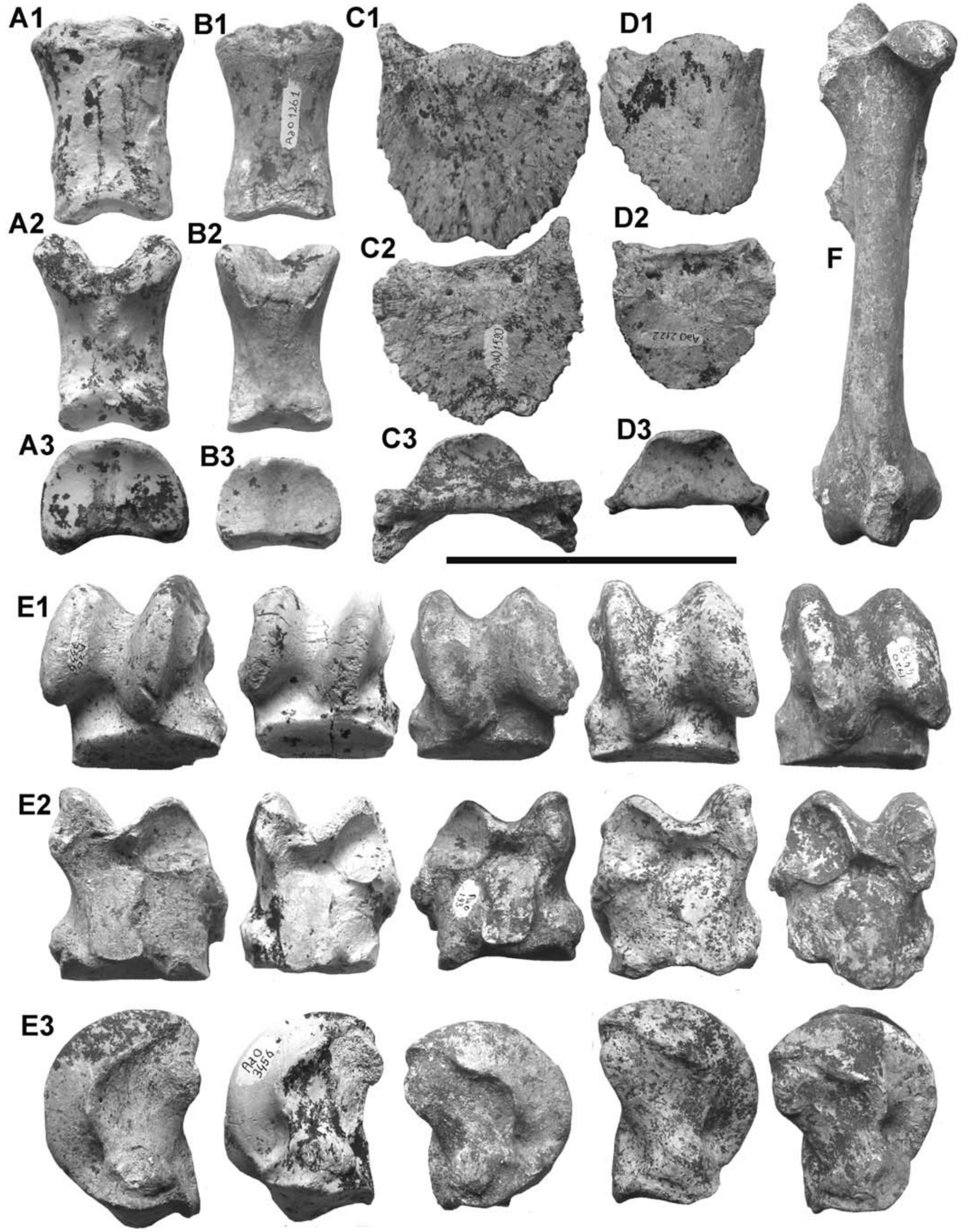

Figure 23. *Hipparion pomeli* sp. nov. from Ahl al Oughlam. **A–D**, phalanges in (1) dorsal, (2) palmar/plantar, and (3) proximal views. **A**, first phalanx AaO-2844; **B**, first phalanx AaO-1261; **C**, third phalanx AaO-1520; **D**, third phalanx AaO-2122. **E**, Astragalus in (1) dorsal, (2) plantar, and (3) medial views; from left to right AaO-3336, AaO-3456, AaO-193, AaO-1530, AaO-4438. **F**, Femur AaO-1503 in dorsal view. Scale bar = 20 cm for Fig. F; 10 cm for all others.

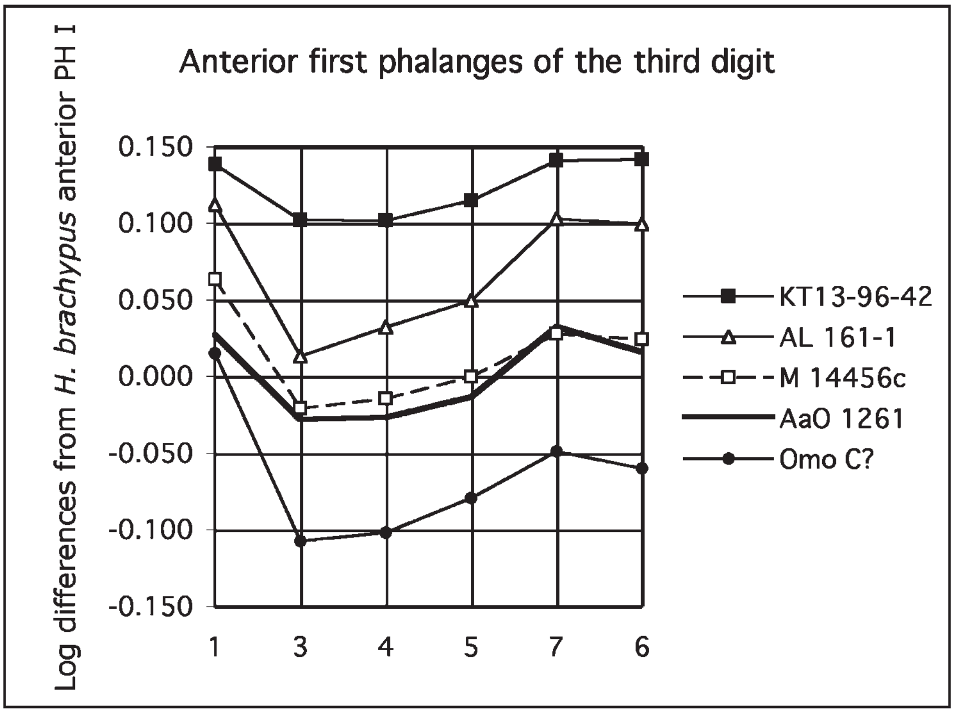

Figure 24. Ratio diagram comparing first anterior phalanges of the third digit. Data in Table 16.

morphologies may be found also in *H. prostylum* of Lubéron, and even in China (AMNH 35 B 255). This kind of structure is obviously related to grazing (Eisenmann 1998) and may well have developed in parallel in more than one lineage. But the extreme pattern, with loss of the third incisors and a broad, square incisival arcade, was achieved only by very late African hipparions (Cornelia and Olduvai, possibly East Turkana Burgi member) and seems to be the second synapomorphy. Indeed, it is this pattern that was first used to define *'Eurygnathohippus'*. *Eurygnathohippus*-like symphyses and ectostylids are not necessarily associated: ectostylids are present in *H. pomeli,* but there is no reduction of the third incisors and the incisival arcade is rounded.

In *H. houfenense s.s.* (THP 10508 and THP 10733. Qiu, pers. comm.; Qiu *et al.* 1988), the muzzle is long and narrow. *H. huangheense* (FAM 11820) is larger, and its muzzle is wider. *H. crusafonti* of Villaroya seems close to the latter species. *H.* cf. *crusafonti* of Kvabebi is smaller, with a short but not very wide muzzle (Fig. 30). *S. perimense* and *H. turkanense* have rounded and rather narrow arcades.

To summarize, in our opinion the name of *Eurygna-*

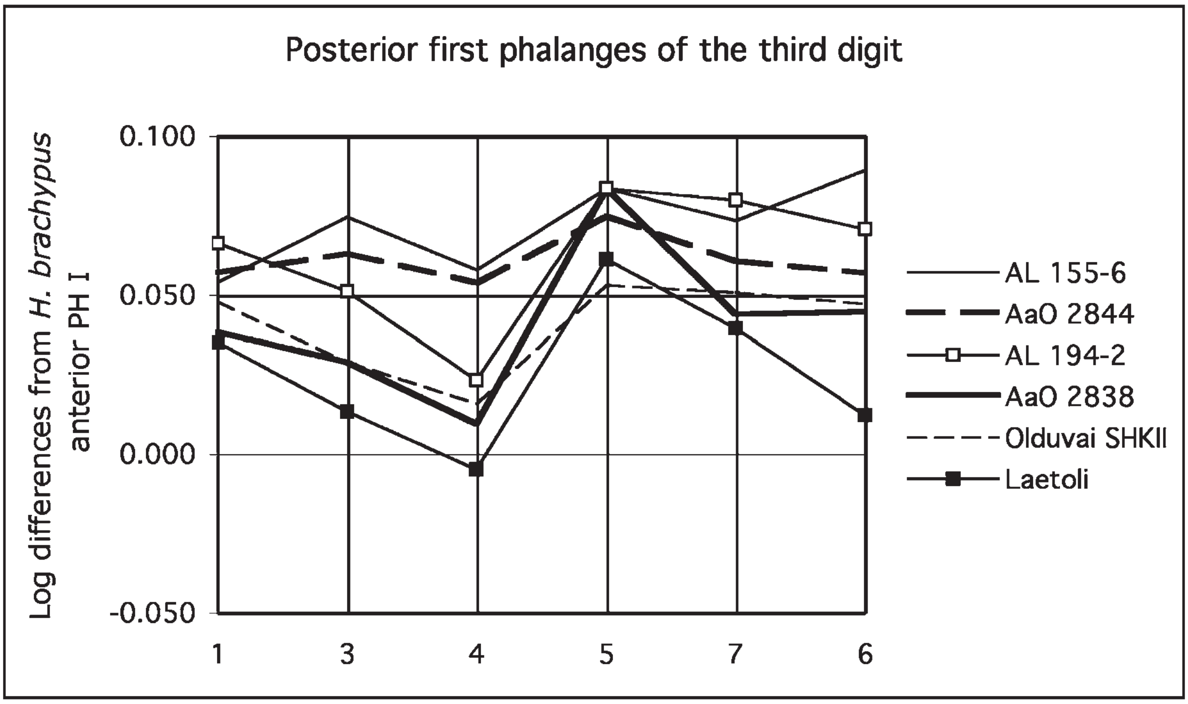

Figure 25. Ratio diagram comparing first posterior phalanges of the third digit. Data in Table 16.

Table 17. Second phalanges of the third digit (PH II).

PH II	Anterior	AaO 1536	AaO 3346	AaO 3912	AaO 4429	
Maximal length	1	42.5		44.2	45.7	
Anterior length	2	34.4	36.2		36.9	
Minimal width	3	36	[39]	37.6	40	
Proximal width	4	43	46.5		45.7	
Proximal depth	5	27.7	30.3		30.4	
Distal width	6	40.8		42.6	44.3	
	Posterior	**AaO 126**	**AaO 196**	**AaO 1268**	**AaO 2842**	**AaO 2847**
Maximal length	1	44	44.5	43.5	41.5	42.5
Anterior length	2	37	34.6	34.3	38	34.7
Minimal width	3	38.3	35.5	35.4	36.2	35.3
Proximal width	4	47	44	43.2	46	42
Proximal depth	5	32	30	30	31	27.7
Distal width	6	39.5	40	38	38.5	39.5

Table 18. Third phalanges of the third digit (PH III).

PH III		Anterior			Anterior?						
		AaO 1519	AaO 1520	AaO 3724	AaO 1547	AaO 2121	AaO 2837	AaO 2846	AaO 3371	AaO 3372	AaO 4430
Length	1		57.5			57.5	55	58	48	49.5	
Anterior length	2		66.5				57	63	58.5		
Height	3		41.8				40	43.5	40	39	
Solar width	4		70.2	74		76	65.5	66	70.3	66.5	
Articular W	5	43.8	45	46	43	48	41	42.5	43.5	44	
Articular depth	6	22.8	25.4	23.3				24.5	23.5	25.5	25
Solar circumf.	7		158			170					

		Posterior		Posterior?					?	Anterior	Posterior
		AaO 2120	AaO 3377	AaO 177	AaO 1284	AaO 2122	AaO 2289	AaO 3703	AaO 2856	AL 155-6 V	AL 155-6 Y
Length	1	55.5	51	50		53.5	60	54.3		68	69
Anterior length	2	58				53		56		85	71.5
Height	3	36.5	36.5			37.2		36.1		54	54
Solar width	4	64	55			54.5				82	76
Articular W	5	38	37			41.5			42	52.5	47.5
Articular depth	6		25.5		23.5	24.7				26	27.5
Solar circumf.	7									200	185

thohippus should be applied only to hipparions that present a derived basicranium, i.e. pointed vomer and long basion–vomer distance. *H. hasumense s.l.* (normal posterior border of vomer situated at subequal distances from basion and palate) is probably a sister group to *Eurygnathohippus.* Their origins are presently unknown.

Our second point of disagreement concerns the derivation of several African hipparions from *H. turkanense.*

Both *H. hendeyi* and *H. feibeli* differ from *H. turkanense* in their slender limb bones. Moreover, *H. hendeyi* (Fig. 27) strongly differs from *H. turkanense* in its very short basion–vomer and orbit–POF distances (Fig. 30, no. 4 and O–POF).

Hipparion sp. of Chad Kossom Bougoudi (Fig. 28) differs from *H. turkanense* in the presence of a POF, relatively close to the orbit (but not as close as that in *H. hendeyi*).

The derivation of *H. hasumense* from *H. turkanense* would imply a notable reorganization of the skull (Fig. 33) besides the acquisition of ectostylids. Such an evolution is possible but still hypothetical.

2. Discussion of Zouhri & Bensalmia's (2005) opinions

Our main disagreement concerns *Eurygnathohippus.* The amended diagnosis of Zouhri & Bensalmia comprises: large size, lack of POF, short naso-incisival notch, long and narrow muzzle, caballine basi-cranium, very hypsodont teeth, constant ectostylids associated with caballoid patterns in lower cheek teeth. Thus defined, *Eurygnathohippus* comprises three species: *E. libycum*, *E. cornelianum,* and *E. afarense* (including *E. hasumense* as a synonym). Zouhri & Bensalmia refer the AaO hipparion to *E. lybicum.* We think that this diagnosis is incorrect:

a) The large size is not a good character: hipparions of Shungura F member and Koobi Fora KBS member, although presumably belonging within *Eurygnathohippus* sensu Zouhri & Bensalmia, were small (Figs 13 & 14).

b) The degree of indentation of the naso-incisival incisure is defined by three points: prosthion, apex of the incisure and anteriormost point of the orbit. Length of naso-incisival notch (no. 30) is the distance between the first two; cheek length (no. 31) is the distance between the last two. The naso-incisival notch is short when it is

Table 19. Measurements of limb bones from Ahl al Oughlam.

Humerus	AaO 73	AaO 1641	AaO 1652	AaO 2194	AaO 2907	AaO 2938	AaO 3341	AaO 4069
Diaphysis width	37						27.6	38
Distal articular width	72			73	76.5	75	69	75
Distal medial depth	77.5				87		76	84
Min. trochlear height	36.3	37.2	36.6	35	37.3	34.5	31.5	38
Radius	*n*	$\bar{x}$	min	max	s.e.	c.v.	Femur	AaO 1503
Maximal length	2	304	297	311	9.9	3.26		375
Medial length	2	289	283	295	8.48	2.94		340
Diaphysis width	3	42.3	40.5	43.3	1.54	3.64		34.8
Proximal width	11	73.0	67	78.2	2.83	3.88		
Proximal articular W	9	69.5	64.8	72.1	2.12	3.04	pr.art.depth	53.7
Proximal depth	6	38.5	36.3	40	1.49	3.87		
Distal maximal width	1	65.5						94.5
Distal articular width	1	60.5						
Distal articular depth	4	34.5	32.5	36	1.48	4.3		
Radial condyle width	4	23.7	22.7	25	1	4.23		
Ulnar condyle width	2	14.5	13	16	2.12	14.63		
Tibia	*n*	$\bar{x}$	min	max	s.e.	c.v.		
Diaphysis width	10	47.4	46	53	2.99	6.31		
Diaphysis depth	8	33.5	31.4	35	1.64	4.89		
Distal width	8	70.9	68	73	2.03	2.87		
Distal depth	10	49.4	48.2	54	2.26	4.57		
Calcaneum	*n*	$\bar{x}$	min	max	s.e.	c.v.		
Proximal length	1	76.5						
Minimal width	12	21.3	17.5	23.3	1.84	8.63		
Maximal width	12	51.6	47	53.3	1.74	3.37		
Proximal width	1	35.5						
Proximal depth	1	57						
Distal depth	10	52.4	47	59.0	3.22	6.15		

smaller than the cheek length (no. 30 < no. 31). This is observed in *H. cornelianum* of Koobi Fora (Appendix Table 2) and *H. hasumense* of Olduvai Bed II (Table 1). The naso-incisival notch is long in *H. hasumense* of Hadar; the two lengths are equal in *H. pomeli* (Table 1). In consequence, the length of naso-incisival notch is not a good character for a diagnosis of *Eurygnathohippus.*

c) Figure 6 shows that the muzzle is long and narrow in *H. hasumense,* but somewhat shorter and wider in *H. cornelianum.* Thus a 'long and narrow muzzle' cannot be mentioned in a diagnosis of *Eurygnathohippus.*

d) As pointed out above, the basi-cranium of our *Eurygnathohippus* is 'hypercaballine' with a remarkably long basion–vomer distance. Moreover, the morphology of the vomer posterior border is quite peculiar in *H. afarense* and *H. cornelianum.* This is absolutely not the case of *H. pomeli* of AaO (Fig. 2, no. 4).

e) 'Very hypsodont teeth' is a vague definition. As shown in Figs 10 & 11, many teeth referred to *Eurygnathohippus* by Zouhri & Bensalmia are only moderately hypsodont, or even not hypsodont when compared with other African hipparions.

Thus, we disagree as to the validity of the genus *Eurygnathohippus* as defined by Zouhri & Bensalmia (2005), since the various species referred by them to this genus display too many and too important differences.

Another point is the inclusion of the AaO *Hipparion* in the species *H. libycum.* This species is based upon two

Table 20. Articular lengths (in mm) of Humerus (H), Femur (F); maximal lengths of Radius (R), Tibia (T), third metacarpal (MC), third metatarsal (MT), first anterior and posterior phalanges of the third digit (PH IA and PH IP); solar width of third anterior phalanx of the third digit (PH IIIA). For Höwenegg, data from Bernor *et al.* (1997), and V.E., unpubl. data.

	H	F	R	T	MC	MT	PH IA	PH IP	PH IIIA
Höwenegg	261.8	367	282.9	364.6	212.8	242.5	65.5	64.8	64.5
AL 155-6	281		332.5	392.5	267	296	75.5	70	82
Çalta	256.5	387	297.3	375	200.4	234.7	68.7	67	76
Ahl al Oughlam		331	304		237.6	282.3	68.8	68.8	74
AaO juveniles ?					230	275	65.8	62.4	
Ahl al Oughlam all		331	304		233.8	278.7	67.3	65.6	74

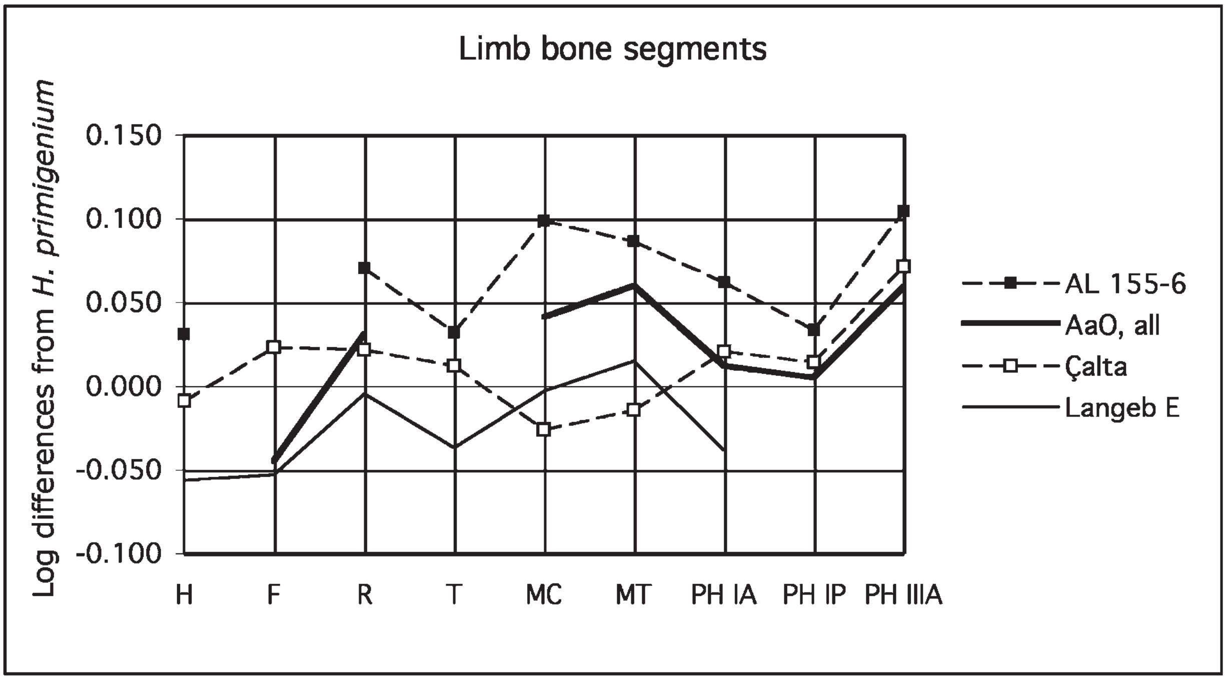

Figure 26. Ratio diagram comparing limb bone segments in hipparions. Data in Table 20.

lower premolars from Algeria, of which we hereby select the one better illustrated by Pomel (1897, plate 1, fig. 5-7) as lectotype (not holotype as stated by Zouhri & Bensalmia). Given the difficulties in *Hipparion* systematics, it is clear that this material does not allow for confident referral of any other specimen to the same species. Therefore, to avoid mixing of several unrelated species within the same species name, the name *Hipparion libycum* should be restricted to the type.

CONCLUSIONS

In our interpretation, over the last 7 Ma there were, in Africa, at least five kinds of hipparions:

— *H. turkanense* of Lower Nawata (Bernor & Harris 2003) has normal basi-cranial proportions (Fig. 33). A very faint POF is placed very far from the orbit. Resemblances between the skull of *H. turkanense* and that of *S. perimense* (AMNH 19761, formerly named *Cormohipparion antelopinum*) do exist and were illustrated by ratio diagrams a long time ago (Eisenmann 1982, fig. 5). It is quite possible that *H. turkanense* derives from *S. perimense* from which it seems to differ mainly by the lack of, or a very faintly marked, POF. But we lack information on *S. perimense* basicranial proportions. Unfortunately, we have no photographs of the Lower and Upper Nawata cheek teeth at our disposal other

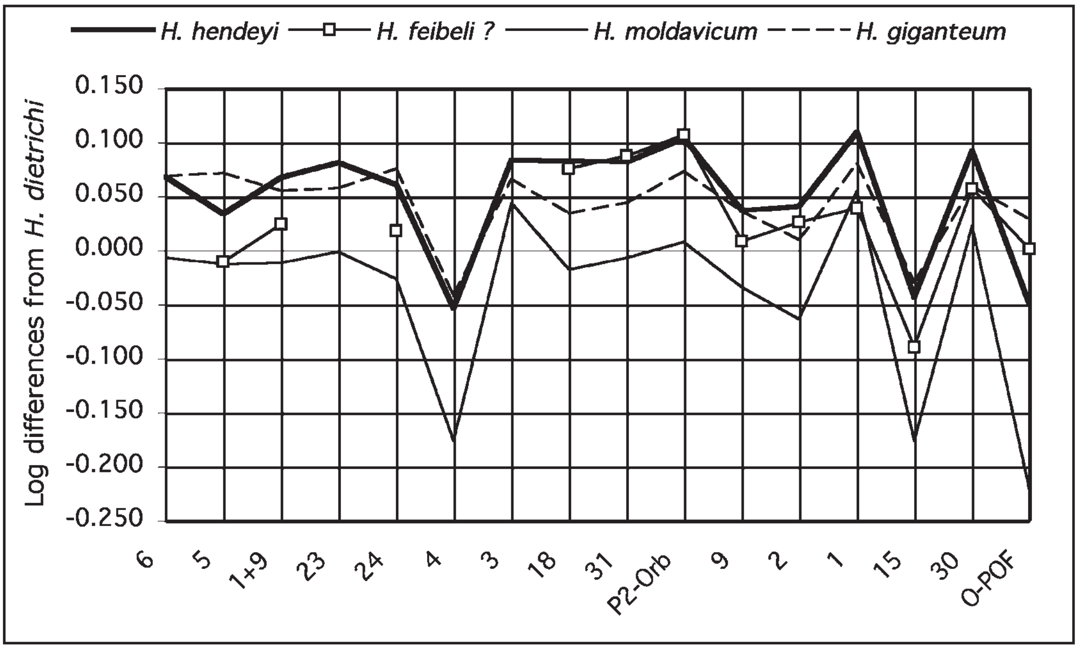

Figure 27. Ratio diagram comparing the skulls of Langebaanweg E, Ekora-Kanam, *Hipparion giganteum* of Grebeniki and *H. moldavicum* of Taraklia. Data in Table 1 and Appendix Table 2.

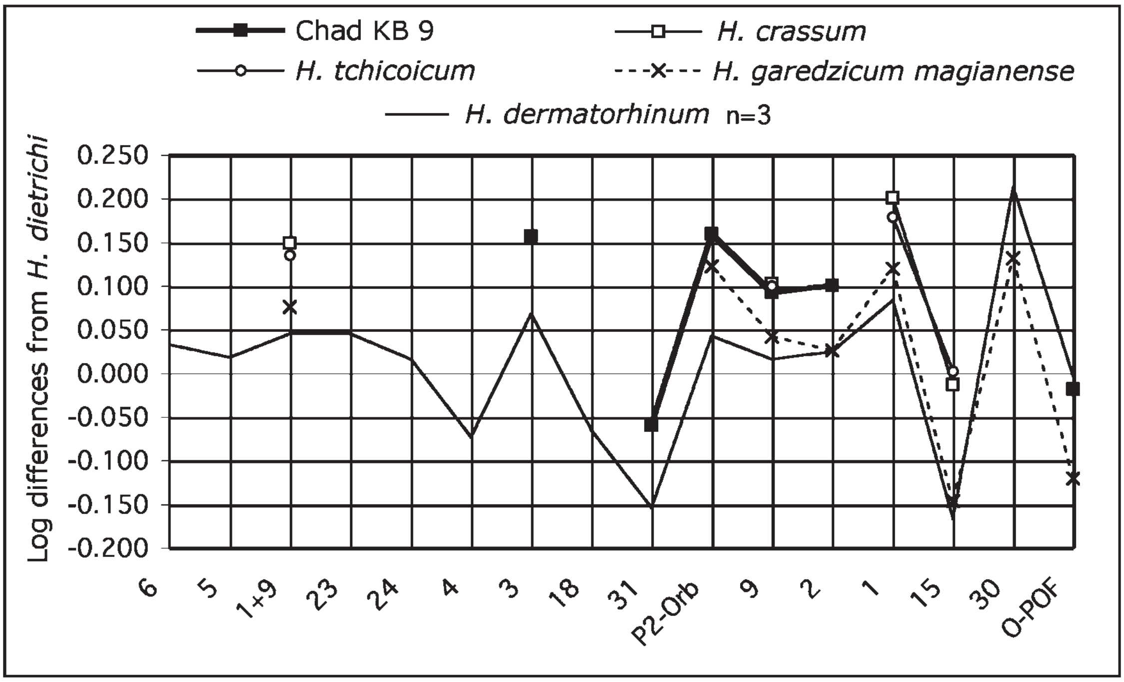

Figure 28. Ratio diagram comparing the skulls of Chad Kossom Bougoudi, *Hipparion dermatorhinum*, and *H. crassum*. Data Bernor *et al.* (1990) and V.E. unpubl. data for *H. dermatorhinum.* Other data in Tables 1 & 2.

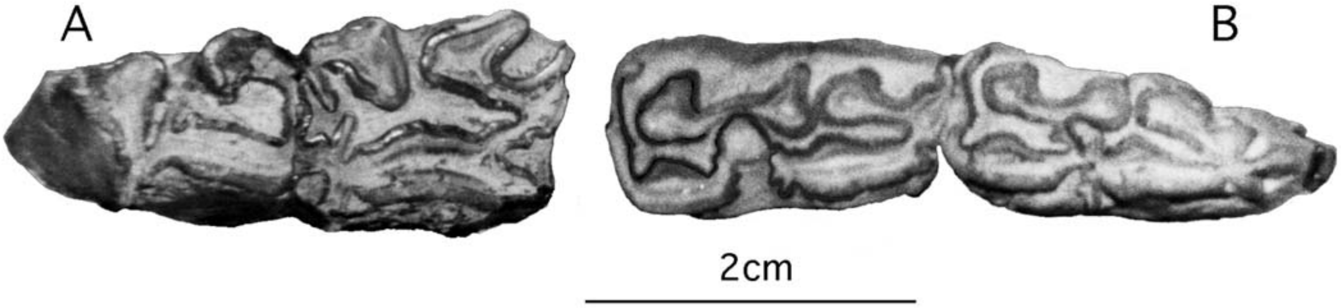

Figure 29. *Hipparion* cf. *crusafonti*, Kvabebi. **A**, dp2, **B**, m2-m3.

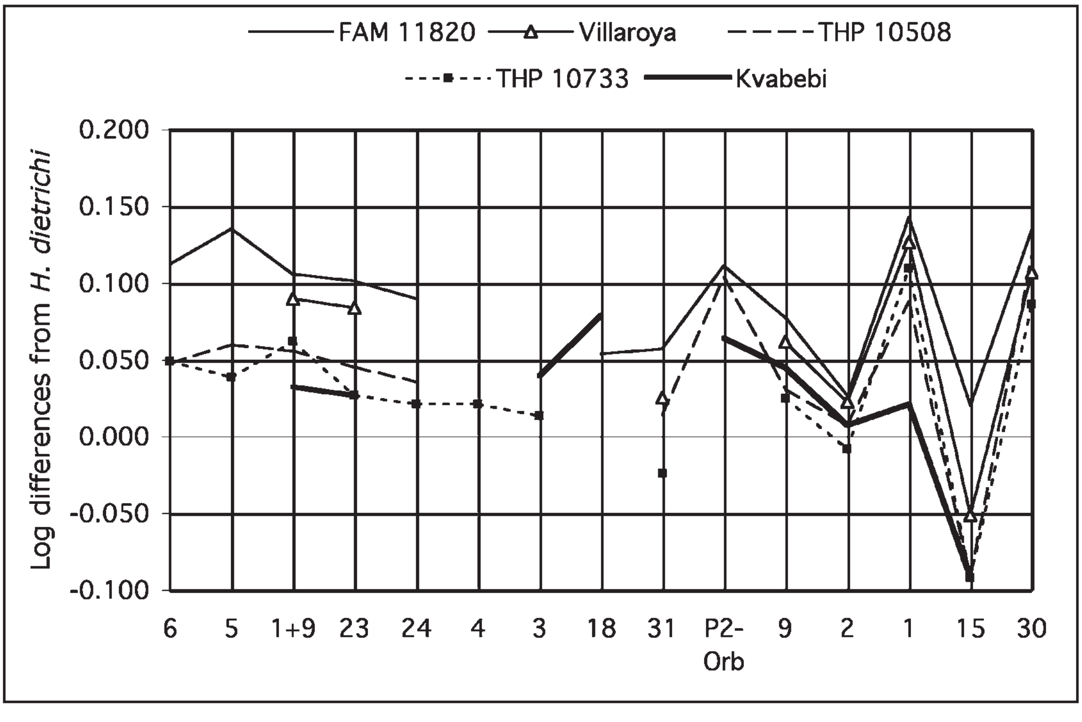

Figure 30. Ratio diagram comparing the skulls of *Hipparion houfenense s.l.*, Villaroya, and Kvabebi. Data in Table 1.

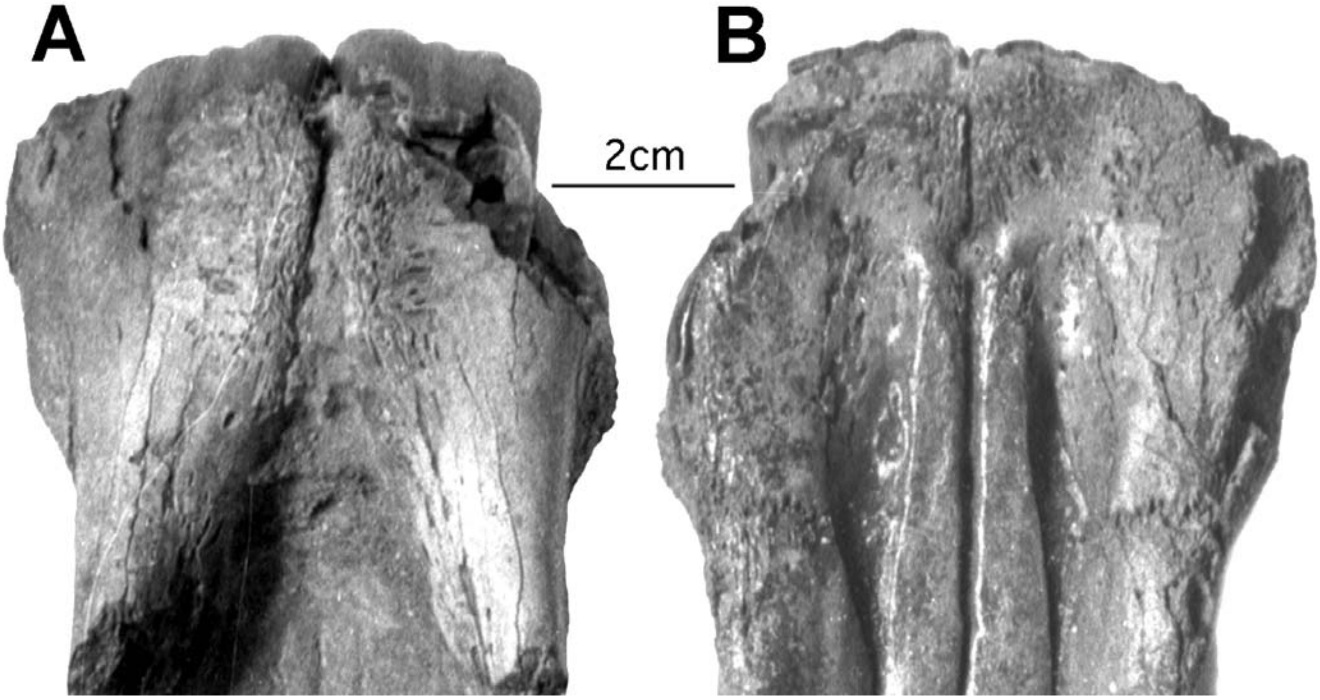

Figure 31. Muzzle KNM-ER 3539; **A**, dorsal view, **B**, ventral view.

than the very worn series from the type skull of *H. turkanense.*

— *H. hendeyi* and *H. feibeli*?. Two European skulls are similar to that of *H. hendeyi* (Fig. 27). They belong to the somewhat smaller *H. moldavicum* of Taraklia, and to *H. giganteum* of Grebeniki. They have short basion–vomer distances and narrow muzzles; the POF of *H. hendeyi,* however, is placed closer to the orbit than in *H. giganteum* and not as close as in *H. moldavicum.* The upper cheek teeth have small and rounded protocones; the lower cheek teeth are hipparionine (Hendey 1978). *H. hendeyi* cannot be derived from *H. africanum* because of its very short naso-incisival notch (Fig. 32). It may have derived from another immigrant. The skulls from Ekora and Kanam, possibly referable to *H. feibeli* but poorly known, may be akin.

— *Hipparion* sp. of Kossom Bougoudi (Fig. 28). It is represented by one of the largest skulls of hipparion. Unfortunately, the teeth are greatly worn. We do not know whether the Chad skull is derived from the *Hippotherium* complex of Bernor & Armour-Chelu (1999a) because of it resemblences with

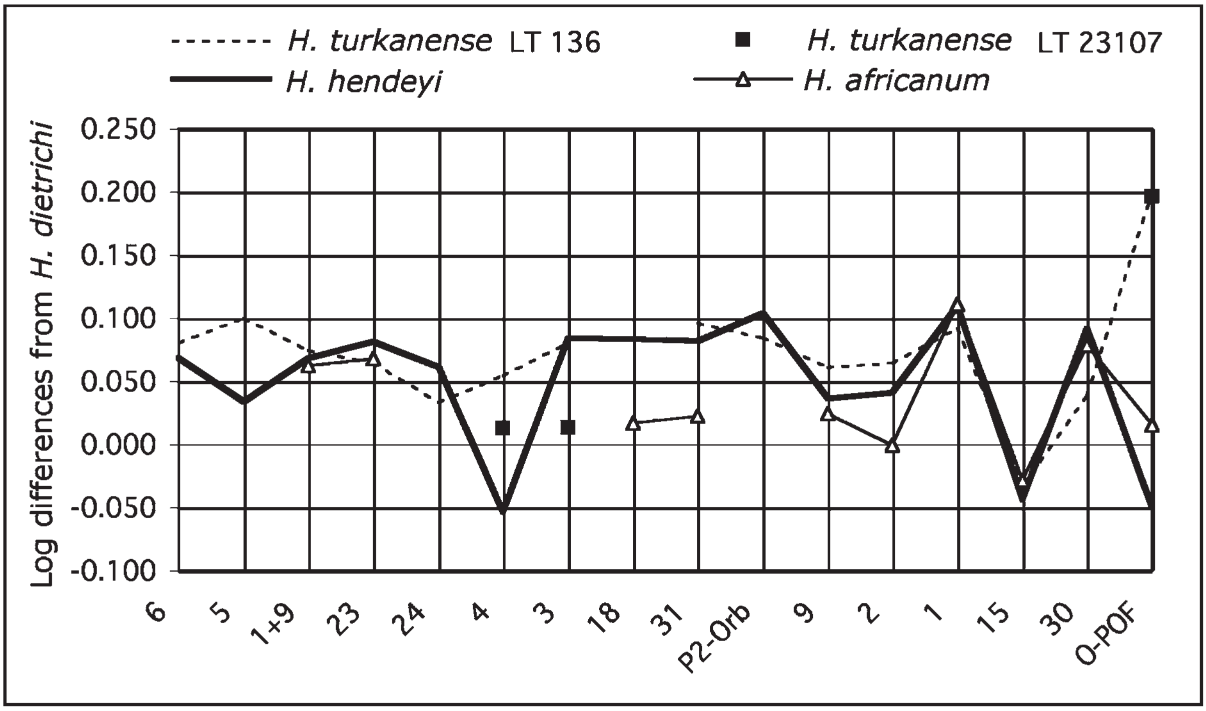

Figure 32. Ratio diagram comparing the skulls of *Hipparion turkanense, H. hendeyi,* and *H. africanum.* Data Bernor & Harris (2003) for *H. turkanense.* Other data in Table 1.

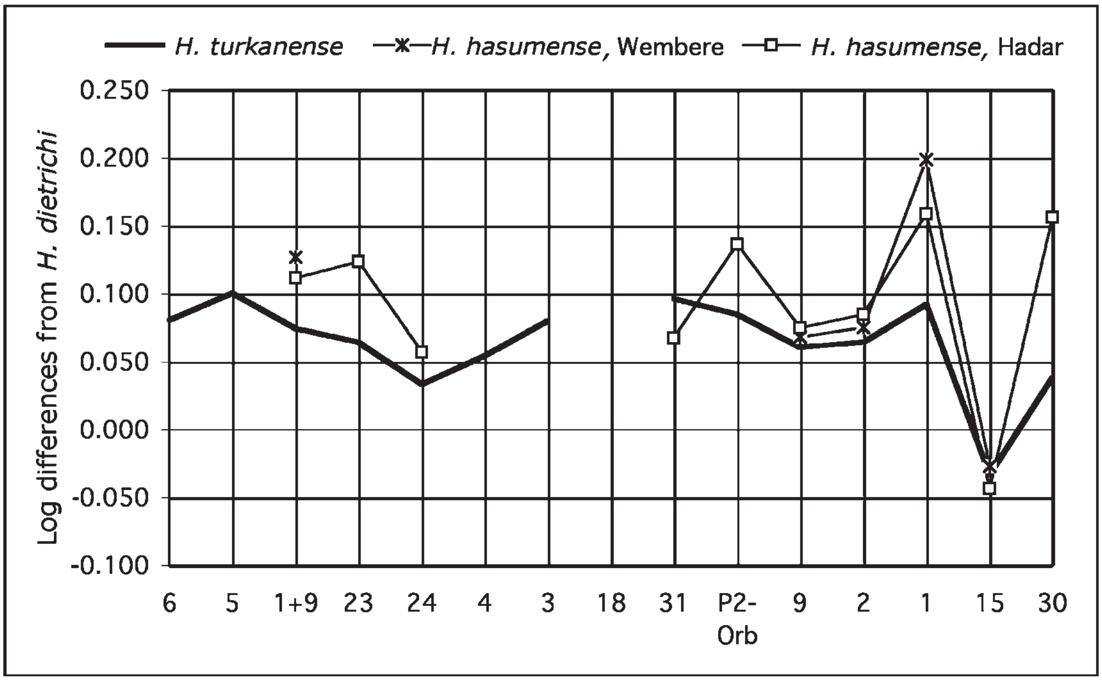

Figure 33. Ratio diagram comparing the skulls of *Hipparion turkanense* LT 136 and *H. hasumense* of Wembere Manonga WW 1528/92 (Data Bernor & Armour-Chelu 1997) and AL 340-8 of Hadar.

H. dermatorhinum in many ways, or from the *Sivalhippus* complex (Bernor & Armour-Chelu 1999b) because of its similarity to *H. crassum s.l.*

— *H. hasumense* group (Figs 2 & 3). This group displays several apomorphies: short cheek, deep naso-incisival notch, caballine double knots, isolated ectostylids and protostylids. Vomer and basi-cranial proportions are normal. The muzzle is long and narrow. We recognize it at Wembere Manonga, Hadar, Ahl al Oughlam (*H. pomeli*), and possibly Olduvai (complete but badly preserved skull BK II 2845/6).

— *H. afarense* and *H. cornelianum* (Figs 4 & 5). As already noted, the structure of the vomer is unique: the acutely pointed vomerian incisure is associated with 'hyper-caballine' basi-cranial proportions. The muzzle is short and wide. Other apomorphies are like those in *H. hasumense.*

It is quite probable that *H. afarense* was the ancestor of the true *Eurygnathohippus* for two reasons: 1) the skulls AL 363-18 of *H. afarense* and KNM ER 3539 of *H. cornelianum* are quite similar; 2) KNM ER 3539 is about 1–2 years old by *Equus* standards (Klingel & Klingel 1966); at that age the permanent I1 (contra Bernor & Armour Chelu 1999a) are erupting and they can perfectly be seen on this skull because the DI1 are lost; an unerupted right I2 may be seen for the same reason, and there is no room for an I3 other than a very reduced one (Fig. 31).

Bernor & Armour-Chelu (1999a) believe that the preceding forms may derive from *H. turkanense,* which they consider as an *Eurygnathohippus*, sister group to *S. perimense.*

In our opinion, the derivation of *Eurygnathohippus* from *H. turkanense* is, for the moment, an assumption based more on the belief that there were no other immigrations of hipparions into Africa than on osteological evidence.

If the Pliocene African hipparions are not descended from *H. turkanense,* they must have an Eurasian origin, and have immigrated into Africa around the Mio-Pliocene boundary (Fig. 34). This period documents indeed a major turnover in African mammalian faunas, mostly by local evolution from local forms. However, there are also some newcomers. In North Africa, the Messinian crisis prompted some faunal exchanges across the Gibraltar straits; they are best known for rodents, but probably involve also canids, and it is likely that a better knowledge of North African Mio-Pliocene large mammals would increase the list. Other taxa of Eurasian origin, arriving in Africa at this time are the Camelidae, first known from the early Pliocene of Chad, and perhaps *Giraffa* and some carnivores: the ursid *Agriotherium,* the hunting hyena *Chasmaporthetes,* and the mustelid *Plesiogulo.* The list is not long, but demonstrates that North–South migrations were possible at that time. The presence at Kossoum Bougoudi, Chad, of a huge hipparion with a very well developed fossa could also result from a migration, possibly of a kind of *H. crassum.*

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ABBREVIATIONS

AaO	Ahl al Oughlam
Hadar DD	Hadar Formation, Denen Dora member
Hadar KH	Hadar Formation, Kada Hadar member
Hadar SH	Hadar Formation, Sidi Hakoma membe
POF	pre-orbital fossa
L	length
W	width

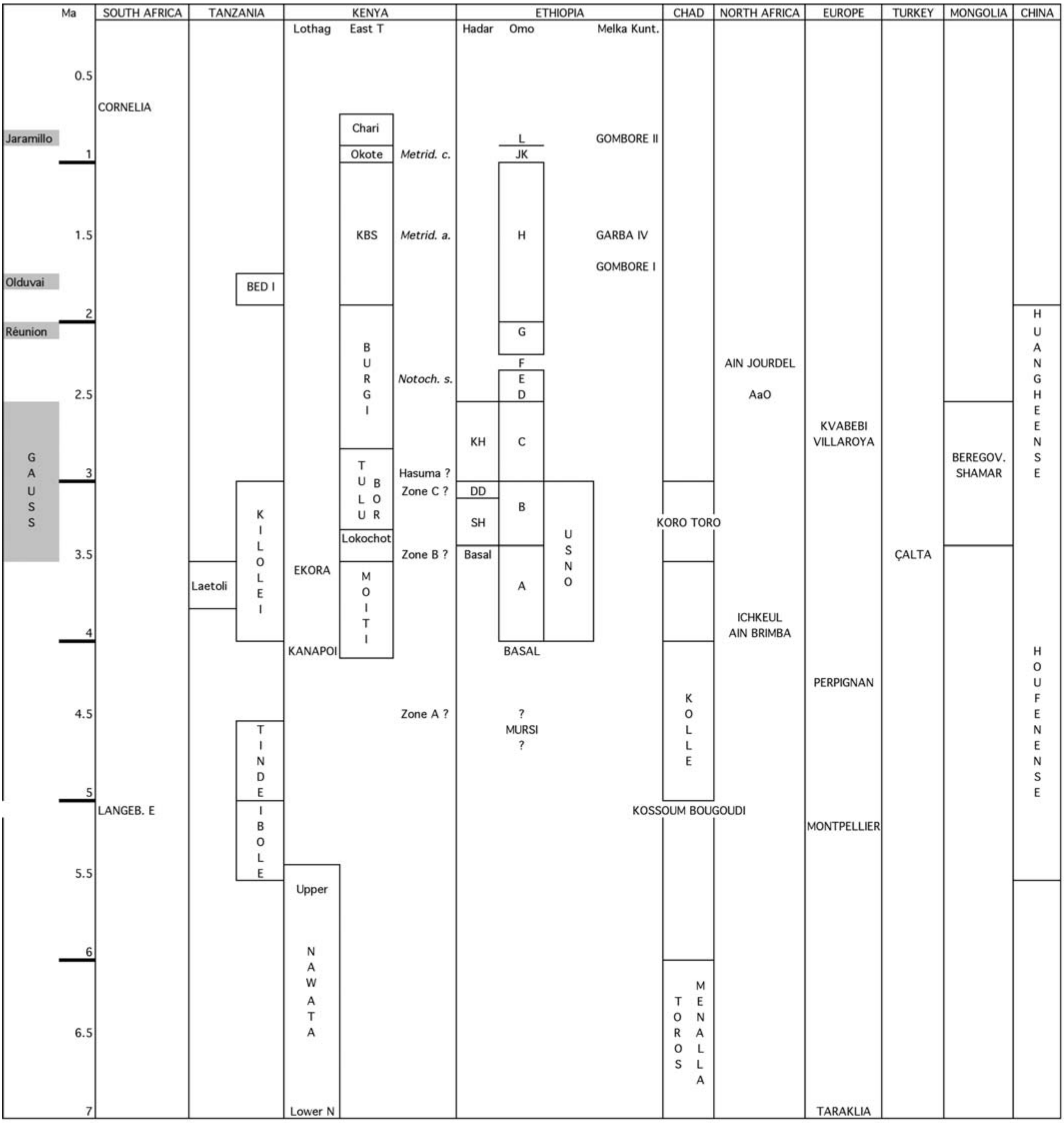

Figure 34. Schematic chronology of some hipparion-bearing late Cenozoic Old World localities.

MC III	third metacarpal
PH I	first phalanx of the third digit
PH II	second phalanx of the third digit
PH III	third phalanx of the third digit
MT III	third metatarsal.

Measurements are in millimetres.

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APPENDIX

Juvenile skulls

Well-preserved skulls are rare. It is frustrating when they belong to juvenile animals, and thus cannot be directly compared to adults. It may, however, be possible to 'extrapolate' the juvenile dimensions to adult ones. We have tried to do so by applying what we know about the skull growth of extant *Equus* species.

Four species were considered: Grevy's zebra, Plains zebras, Hemiones, and Przewalski's horses. Comparison was made between average adult skulls and juvenile skulls of different ages by calculating the percentage rate of 'growth' of the latter. Appendix Table 1 gives the percentages of growth of the dimensions used in our ratio diagrams. The choice of dimensions was made to adapt to more-or-less complete fossil material. Thus, some are simple measurements while others are sums of segments. Most were defined in Eisenmann *et al.* (1988). Appendix Fig. 1 illustrates the values of the percentages of growth in the considered extant species.

Samples of adult skulls were chosen to correspond as much as possible to the available (always poor) juvenile samples. For instance, only adult *E. burchelli* from Etosha Pan were used because the best sample of juvenile skulls comes from Etosha Pan. For adult skulls, means were calculated from *c.* 60 *E. grevyi* (but cheek and naso-incisival notch lengths are known only from five specimens), and *c.* 60 hemiones (excluding hemippes, kiangs, and Mongolian hemiones), 22 to 31 *E. przewalskii,* and 15 to *E. burchelli.* Juvenile samples vary from one age group to another.

The juvenile skulls we examined (Appendix Table 2) are: KNM ER 3539 from East Turkana, BM 5465, and BK II 283 from Olduvai (*H. cornelianum*); KNM EK 4 from Ekora and BM 15906 from Kanam West (*H. feibeli* ?).

One–two years. Juvenile samples consist of 9 *E. grevyi,* 9–10 *E. burchelli,* 6–11 *E. hemionus,* and 7–13 *E. przewalskii.*

Naturally, the highest percentages concern the 'growth' of the cheek teeth, since there are only three decidual teeth instead of six adult. The smallest percentages concern the growth in length of the muzzle. Obviously, skulls of different species grow in different ways. In *E. grevyi* the muzzle width grows less than in other species while the length of the naso-incisival notch seems to increase more. On the whole, however, the concordance seems good enough to justify tentative reconstructions of juvenile skulls.

A perfectly preserved juvenile skull (KNM ER 3539) was found under the KBS Tuff in East Turkana. It was illustrated in Eisenmann (1976, Plate 3). The M1 had begun to wear, the M2 were not erupted. In *Equus,* that would indicate an age of between one and two years. The following ratio diagram (Appendix Fig. 2) compares dimensions of the juvenile skull with tentative reconstructions of its adult state according to the *Equus* species growth. It shows that most of predicted adult dimensions are similar but notable interspecific differences appear in the width of the muzzle.

The use of *Equus* skulls as the basis for a reconstruction of an *Hipparion* skull may appear rash and untestable. We can, however, somehow 'test' the (accuracy of) extrapolation of KNM ER 3539 by comparing it with the adult skull of *H. afarense* AL 363-18 (Eisenmann, 1976, Plate 2). The obvious resemblances on the next ratio diagram (Appendix Fig. 3) make our reconstruction credible. The adult skull ER 3539, when adult, would probably have looked like *H. afarense,* possibly slightly smaller and with longer teeth and palate. The muzzle would have been at least 70.4 mm wide (according to the *E. grevyi* model), possibly as wide as, but no more than, 91.7 mm (*E. przewalskii* model), more probably about the calculated average (81 mm) which is close to the actual width of *H. afarense* (80 mm).

About one year. Juvenile samples consist of one *E. grevyi,* six *E. burchelli,* 2–5 *E. hemionus,* and five *E. przewalskii.*

The juvenile skulls KNM EK 4 from Ekora and BM 15906 from Kanam West are about one year old (unerupted M1). They both have a POF and have also the same dimensions of the deciduous series. We suppose that they belong to the same species. The various possibilities of adult state are represented in Appendix Fig. 4. Their overall concordance justifies the use of an average adult state (Appendix Fig. 5).

One of us has already pointed that the Ekora skull may well belong to the small hipparion of Lothagam (Eisenmann 1995). If so, our reconstruction gives an idea about the adult skull of *H. feibeli* (Bernor et Harris 2003). According to our results, the *H. feibeli* skull most resembles *H. verae* and *H. giganteum* of Grebeniki (as seen on the ratio diagram Appendix Fig. 5), and *H. hendeyi* (Fig. 24).

From Olduvai, there is another fragmentary skull of about one year old, BM 067/5465. Although perhaps slightly younger than KNM ER 3539, it has larger dimensions. Otherwise it does not seem much different. Unfortunately the vomer–basion distance is uncertain. Two alternatives were used (Appendix Fig. 6). It appears that BM 5465 had relatively smaller teeth than KNM ER 3539 but probably belonged also to *H. cornelianum.*

About three years. Juvenile samples consist of 1–15 *E. grevyi,* 4–7 *E. burchelli,* 5–10 *E. hemionus,* and 3–8 *E. przewalskii.*

A fragmentary juvenile skull from Olduvai Bed II, BK II 283, was illustrated by Hooijer (1975, Plates 9–10). P4 and M3 are erupting, which would point in *Equus* to an age of around 3 years. The skull is particularly interesting because it has well preserved frontals. The reconstructions based on our modern models differ but slightly. Like in BM 5465, the teeth are relatively small. We refer it also to *H. cornelianum* (Appendix Fig. 6).

The real (juvenile) and extrapolated 'adult' values are in Appendix Table 2.

Skull-mandible dimensions

Another question concerns the relationship between mandible and skull dimensions, in particular muzzle lengths and widths.

Muzzle lengths. We have calculated the regression line for skull versus mandible dimensions in 83 modern horses (Appendix Fig. 7). The correlation R^2 is 0.88. The skull muzzle length = (0.963 × mandible muzzle length) + 15.8. The Hadar skull of *H. hasumense* AL 340-8 is associated with a mandible. The mandible muzzle length is about 130 mm, the skull muzzle length is about 140 mm. The muzzle length of the mandible AL 177-21 (also from DD) is the same; according to the regression, the skull muzzle length would have been 141.2 mm, i.e. close to the actual length in AL 340-8. For the mandible of *H. cornelianum* KNM ER 1626 (muzzle length 115 mm), the corresponding skull dimension would have been 126.7 mm. For the mandibles of *H. crassum* P. 208 and of *H. tchicoicum* (muzzle lengths 144 and 136 mm), the corresponding skull dimensions would have been 154.8 and 147 mm.

The regression of mandible versus skull dimensions is: mandible muzzle length = (0.910 × skull muzzle length) + 1.022.

Muzzle widths. We calculated the regression lines for skull versus mandible dimensions and of mandible versus skull dimensions in modern equids with broad muzzles to match the broad muzzled African hipparions. The sample comprises 32 horses and 29 kiangs (Appendix Fig. 8). The correlation R2 is 0.80.

- Skull muzzle width = (0.729 × mandible muzzle width) + 21.823.
- Mandible muzzle breadth = (1.097 × skull muzzle width) – 11.959.

In the first scatter diagram (Appendix Fig. 8) are plotted the real values for the associated skull and mandible AL 340-8 of *H. hasumense* and the values estimated from the mandible and from the skull. The real AL 340-8 plots far from the regression line, with an actual skull muzzle 57 mm wide instead of the calculated 61.2 mm. This is probably because it is very old and slightly crushed (Eisenmann 1976, plate 1).

In the same diagram are plotted the values for *H. hendeyi* of Langebaanweg E. The skull L 22187 is old, and its muzzle width is 57 mm, giving 50.6 mm for an estimated width of the mandibular muzzle. On the normal mandible L 20553 the muzzle width is 56 mm giving 62.7 mm as the probably normal skull width.

In Appendix Fig. 9 are plotted the estimations for the skull muzzle widths of AL 177-21 (62.7 mm), Omo 18-1968-363, KNM ER 1626 (73.6 mm), 324 (64.1 mm), and 1221 (67 mm), Olduvai 067/5344, Melka Kunturé Garba IVD 6767, and Cornelia COR 679 (74 mm).

In Appendix Fig. 10 are plotted the estimations for the mandibular muzzle widths of AL 155-6 (53.9 mm), AL 363-18 (64.8 mm), AL 142-18 (68.1 mm), Olduvai BK II 2845/6 (56 mm) and BK II 264 (71.4 mm), WW 1528/92, AaO 3647 (53.9 mm), Lothagam LT 136 (54.7 mm), KNM ER 3539, and Kanam BM 15906.

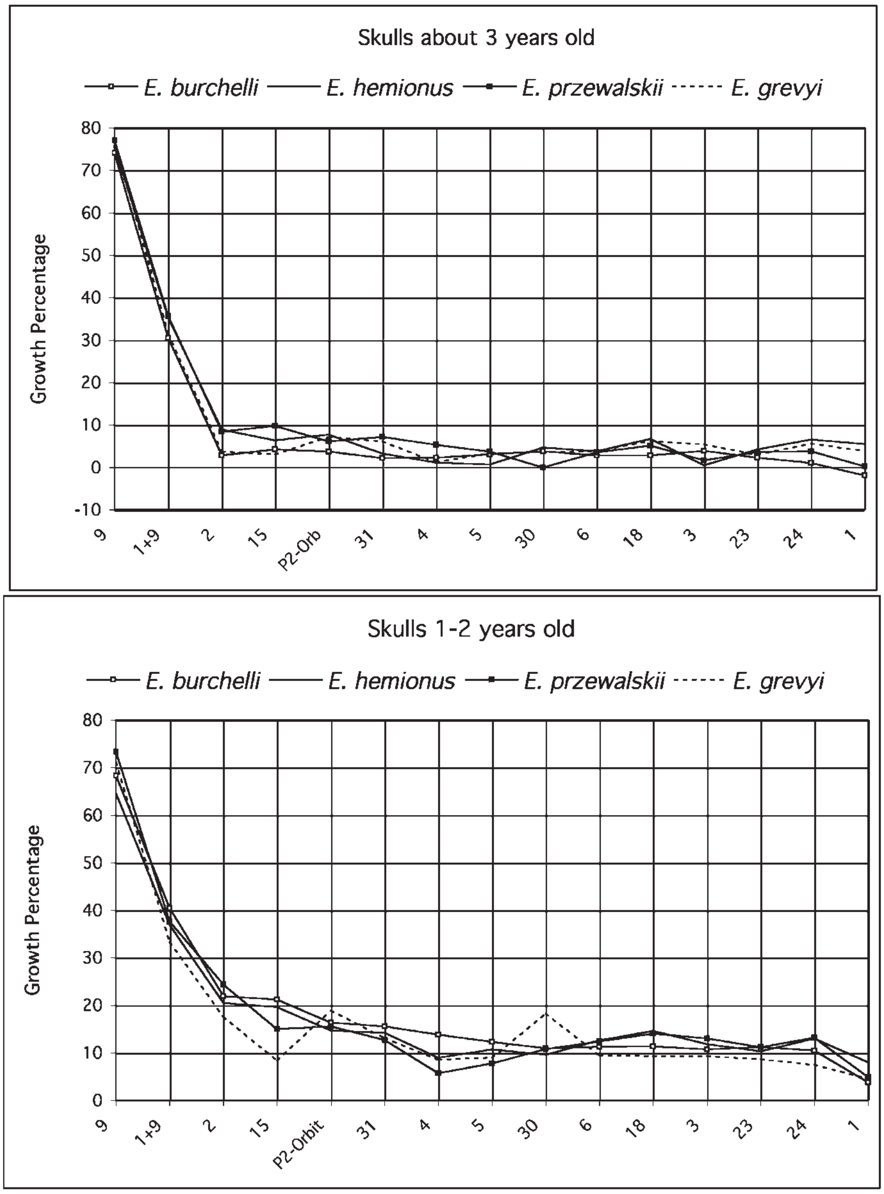
Not plotted estimations for *H. crassum* and *H. tchicoicum* are in Table 2.

Appendix Table 1. Percentage of growth of extant *Equus* species.

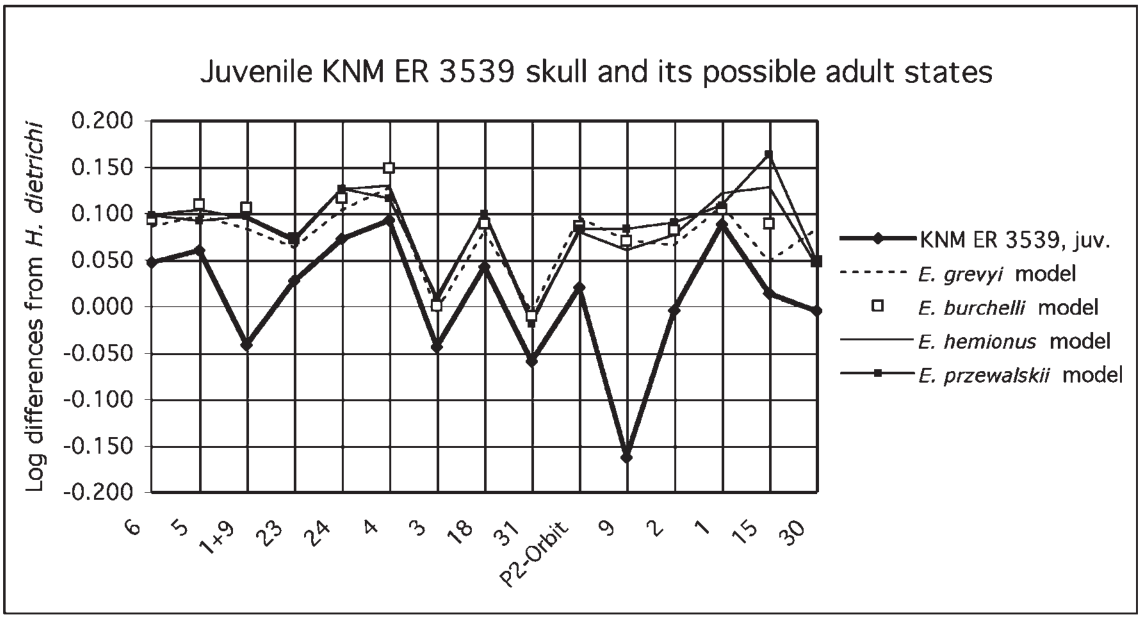
		E. grevyi	*E. burchelli*	*E. hemionus*	*E. przewalskii*
	adults	$n = 5–60$	$n = 15$	$n = 58–59$	$n = 22–31$
	around 3 years	$n = 1–15$	$n = 4–7$	$n = 5–10$	$n = 3–8$
Basilar length	6	3.8	2.8	3.8	3.5
Postpalatal length	5	3.3	3.1	0.7	3.6
Muzzle + cheek teeth L	1+9	31.5	30.5	35.3	35.6
Anterior ocular line	23	3.0	2.3	4.2	3.6
Posterior ocular line	24	5.6	1.0	6.6	3.8
Postvomerine length	4	1.2	2.3	1.1	5.3
Vomerine length	3	5.4	3.9	0.5	1.7
Frontal width	18	6.2	2.8	6.7	5.1
Cheek length	31	6.1	2.2	3.3	7.2
P2–Orbit	P2–Orbit	7.2	3.7	7.7	6.1
Cheek teeth length	9	77.4	74.1	75.6	77.2
Palatal length	2	3.7	2.8	8.9	8.3
Muzzle length	1	3.9	–1.9	5.5	0.2
Maximal muzzle width	15	3.1	4.2	6.4	9.8
Length of narial opening	30	3.5	3.8	4.7	–0.1
	1 to 2 years	$n = 9$	$n = 9–10$	$n = 6–11$	$n = 7–13$
Basilar length	6	9.4	11.3	12.6	12.4
Postpalatal length	5	9.0	12.3	10.7	7.8
Muzzle + cheek teeth L	1+9	33.3	40.4	36.9	37.6
Anterior ocular line	23	8.7	11.2	10.3	11.2
Posterior ocular line	24	7.4	10.5	13.0	13.2
Postvomerine length	4	8.5	13.8	9.0	5.7
Vomerine length	3	9.3	10.7	11.8	13.0
Frontal width	18	9.3	11.4	14.6	14.1
Cheek length	31	13.1	15.6	14.2	12.7
P2–Orbit	P2–Orbit	18.9	16.4	14.7	15.6
Cheek teeth length	9	71.2	68.3	64.6	73.3
Palatal length	2	17.6	21.9	20.5	24.4
Muzzle length	1	4.6	3.8	8.0	4.9
Maximal muzzle width	15	8.4	21.2	19.6	15.0
Length of narial opening	30	18.3	11.0	9.6	10.8
	around 1 year	$n = 1$	$n = 6$	$n = 2–5$	$n = 5$
Basilar length	6	16.3	17.9	18.7	21.5
Postpalatal length	5	15.0	17.5	15.0	16.9
Muzzle + cheek teeth L	1+9	32.1	36.2	39.3	42.5
Anterior ocular line	23	14.0	17.3	15.0	20.1
Posterior ocular line	24	12.7	13.7	18.7	25.0
Postvomerine length	4	3.7	16.5	12.0	9.8
Vomerine length	3	29.0	18.6	24.1	26.2
Frontal width	18	14.8	16.9	23.0	25.6
Cheek length	31	22.3	22.8	20.0	21.2
P2–Orbit	P2–Orbit	32.0	22.8	22.9	31.5
Cheek teeth length	9	59.1	67.4	68.7	75.2
Palatal length	2	36.8	32.4	27.3	33.6
Muzzle length	1	9.1	10.3	12.8	11.2
Maximal muzzle width	15	23.1	21.0	23.4	33.0
Length of narial opening	30	21.0	16.4	20.1	29.0

Appendix Table 2. Measurements in mm of juvenile hipparion skulls.

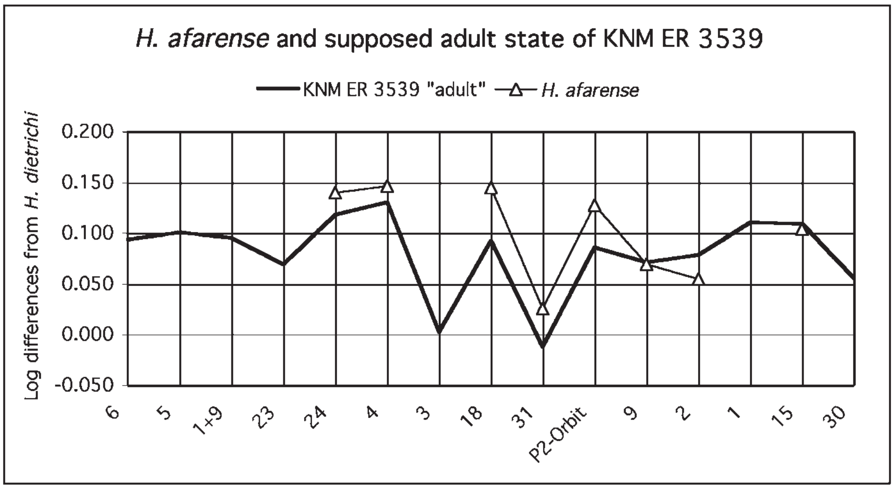
		H. feibeli ?		*H. cornelianum*		
		Ekora *c.* 1 year KNM EK 4	Kanam W *c.* 1 year BM 15906	Koobi Fora Burgi 1–2 years KNM ER 3539	Olduvai BK II *c.* 1 year BM 067/5465	Olduvai BK II *c.* 3 years BK II 283
P2 – Orbit				146		170
Muzzle length	1		96	119		
Palatal length	2	87		110		
Vomerine length	3			85	95	
Postvomerine length	4			128	[139]	
Postpalatal length	5	[165]		210	[234]	
Basilar length	6			430		
Lacteal premolar length	7	86	86	96	100	[90]
Choanal length	10	[57]		62	65	
Minimal choanal width	11	[25]		35	[35]	
Maximal choanal width	12	[37]	[31]	39	[43]	
Minimal muzzle width	14		29	49		
Muzzle width at I3	15		41	[65]		
Length of temporal fossa	16	65				
Frontal width	18	[150]		180	[180]	215
Bizygomatic width	19			[180]		[200]
Basioccipital width	21	[87]				
Anterior ocular line	23			320		
Posterior ocular line	24	148		197	[190]	
Facial height	25		76	88		
Cranial height	26	82		83	105	
Ant–post. orbital diameter	28	51		57	56	
Vent–dors. orbital diameter	29	51		[48]	50	
Length of naso-incisival notch	30		[110]	120		
Cheek length	31			130		
Orbit to preorbital fossa (POF)	32	45				
Length of POF	33	61				
POF to foramen infraorbitale	34	43				
Height of POF	35	34				
POF to facial crest	36	29				
For. infraorb. to alveol. border	37	40				
POF to alveolar border	38	67				



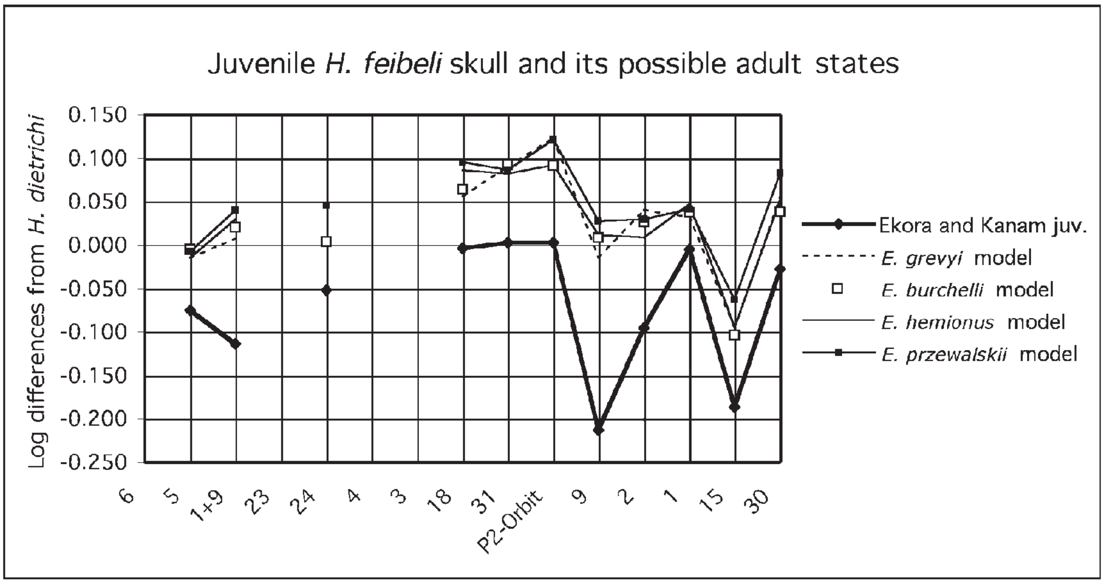
Appendix Fig. 1. Percentage of growth of extant *Equus* species. Measurements defined in Appendix Table 1.



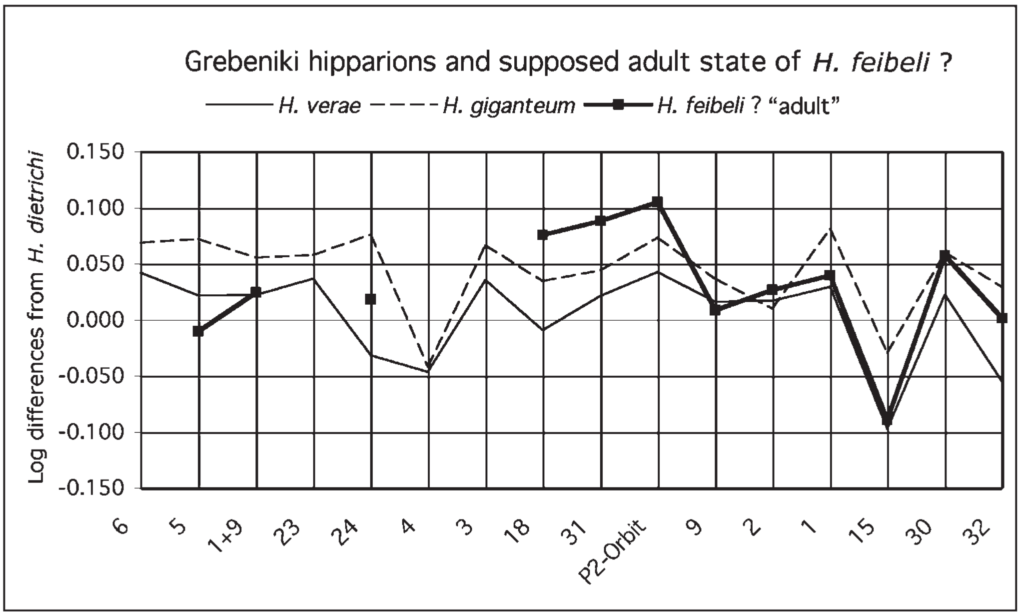
Appendix Fig. 2. Ratio diagram of *H. cornelianum* juvenile skull from Koobi Fora, Burgi and its adult dimensions according to the growth of extant *Equus* skulls.



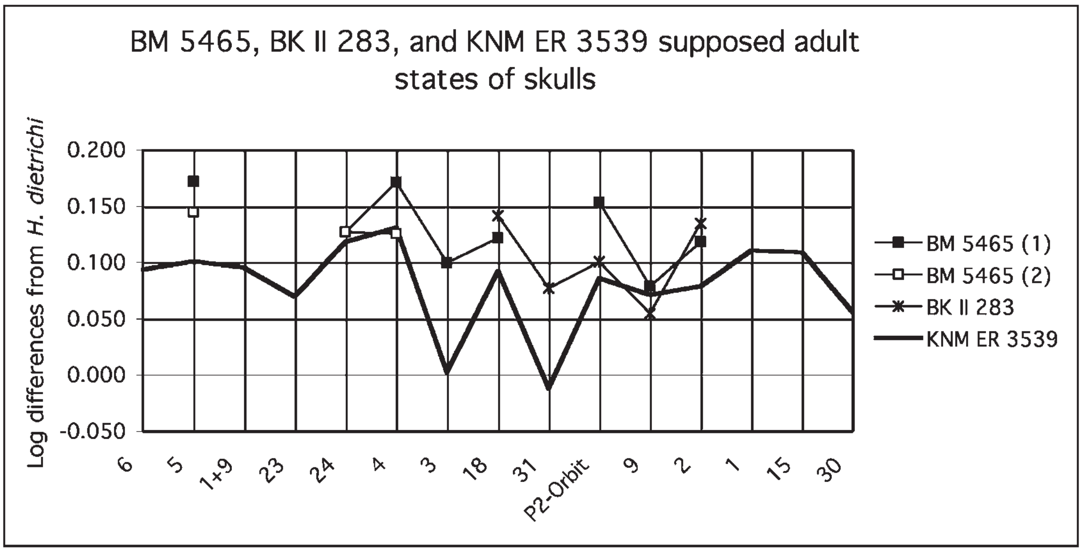
Appendix Fig. 3. Ratio diagram of *H. cornelianum* skull supposed adult dimensions compared to the adult *H. afarense.*



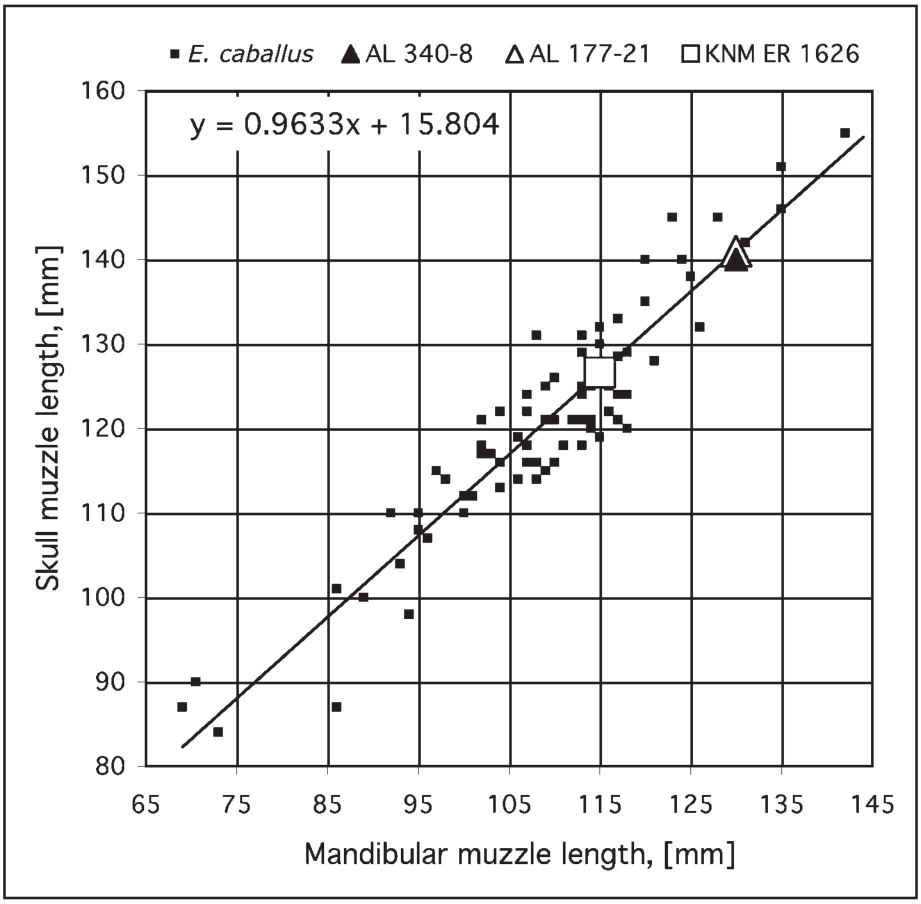
Appendix Fig. 4. Ratio diagram of *H. feibeli* ? juvenile skulls from Ekora and Kanam and its adult dimensions according to the growth of extant *Equus* skulls.



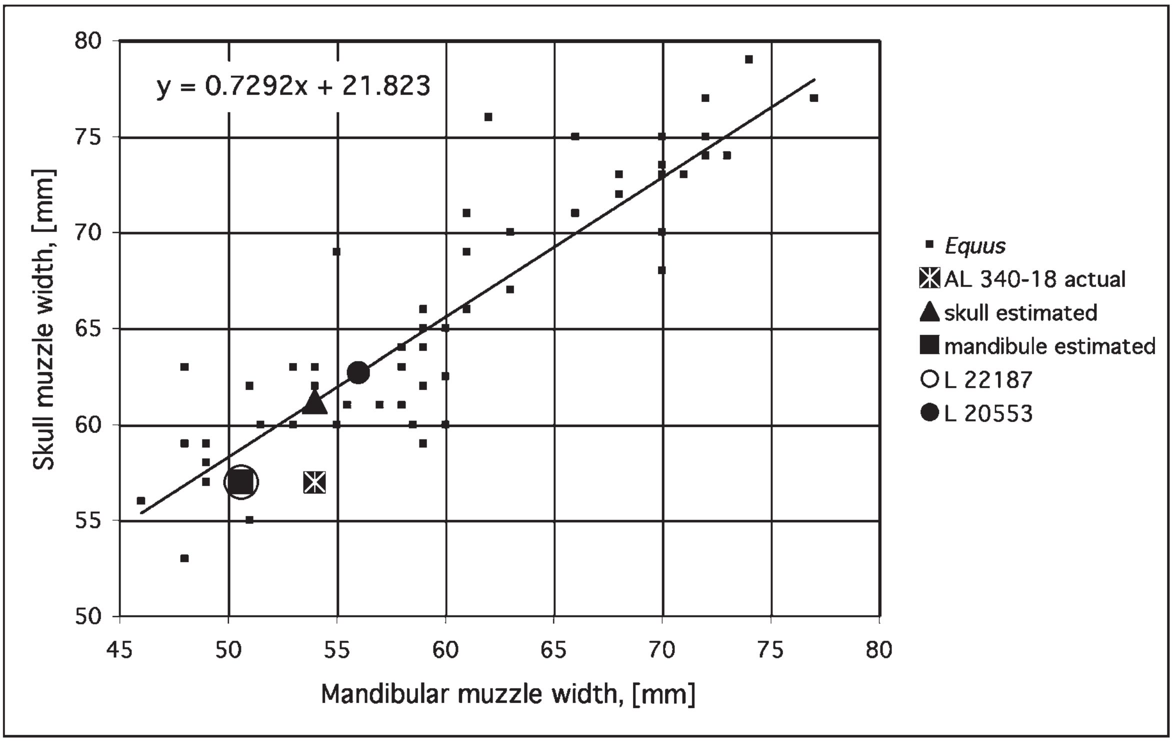
Appendix Fig. 5. Ratio diagram of *H. feibeli* ? skull supposed adult dimensions compared to the adults *H. verae* and *H. giganteum* of Grebeniki.



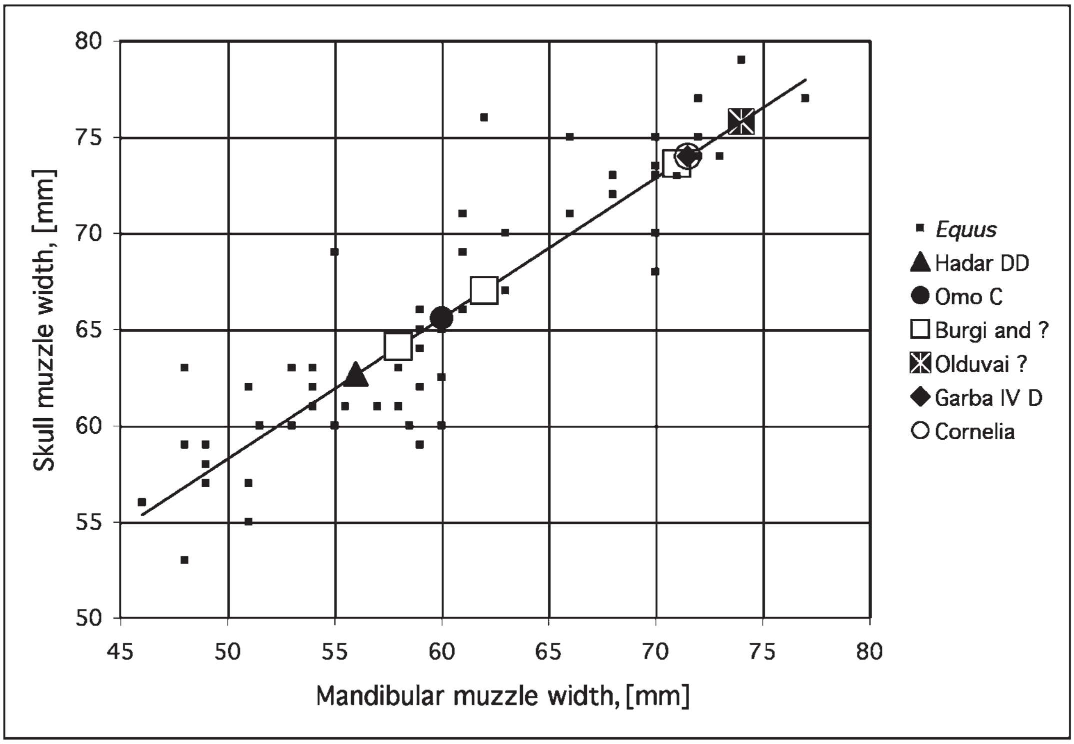
Appendix Fig. 6. Ratio diagram of supposed adult dimensions of *H. cornelianum* from Koobi Fora, Burgi and Olduvai Bed II.



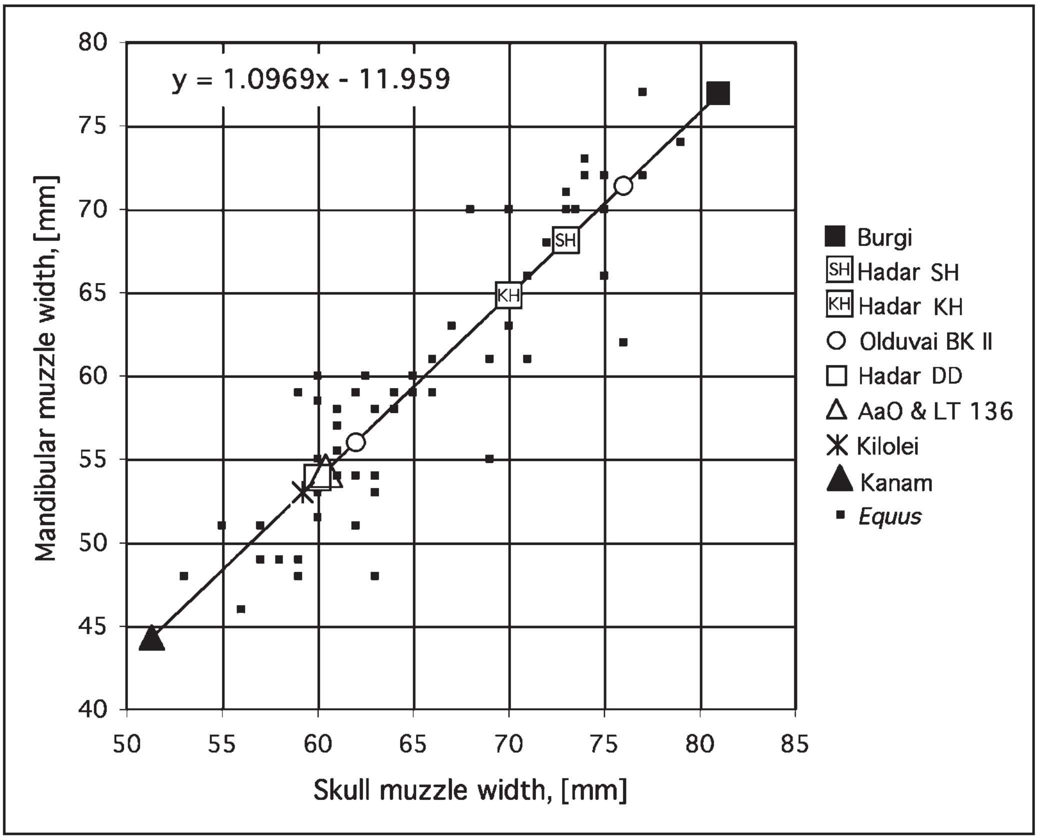
Appendix Fig. 7. Scatter diagram and regression of the skull muzzle length on the mandibular muzzle length.



Appendix Fig. 8. Scatter diagram and regression of the skull muzzle width on the mandibular muzzle width.



Appendix Fig. 9. Scatter diagram and regression of other skull muzzle widths on other mandibular muzzle widths.



Appendix Fig. 10. Scatter diagram and regression of the mandibular muzzle width on the skull muzzle width.